



# The flow regulation services of wetlands

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## ABSTRACT

Wetlands potentially provide a range of ecological (or ecosystem) services including ground water recharge, nutrient retention, waste assimilation, shoreline stabilization, and carbon storage. One of the most cited and valuable services potentially provided by wetlands are their influence on flow regimes, especially flood attenuation and augmentation of low flows. Here we report the results of a meta-analysis of twenty-eight studies, including fifty-nine associated effect sizes, that have investigated the flow regulation services of wetlands. We found that, consistent with conventional wisdom, on average wetlands reduce the frequency and magnitude of floods and increase flood return period; augment low flows; and decrease runoff and streamflow. However, our results also indicate gross wetland characteristics have little predictive power with respect to the observed variation in the level of flow regulation services. This implies that in that in the absence of detailed site-specific information, estimates of flow regulation services provided by wetlands will generally have large uncertainty, as will any associated estimate of their economic value.

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## 1. Introduction

Wetlands are considered to play an important role in hydrological functions and processes that underlie a range of potential ecosystem services. These services include enhancing ground-water recharge, nutrient and chemical retention and cycling, water purification and waste treatment, soil formation, and controlling erosion and sedimentation (Berlin and Handley, 2007; Brauman et al., 2007; Mitsch and Gosselink, 2007). But perhaps the most cited wetland services is their impact on flow regimes, specifically their potential to reduce flood peaks and increase flood return period, augment low flows, and reduce runoff and streamflow. Indeed, Mitsch et al. (1977) have argued that wetlands serve “as nature’s age-old method of flood control” by virtue of their short- and long-term water storage capacity, both of which are expected to reduce downstream flood peaks.

There is evidence that floodplain wetlands reduce the frequency (Acreman et al., 2003 and Hillman, 1998) and magnitude (Ferrari et al., 1999 and Ogawa et al., 1986) of flood events and increase the time to peak of these events (Hardy et al., 2000 and Walton et al., 1996). Similar results have been obtained for head-water wetlands (e.g., Robertson et al., 1968 and Wu and Johnston, 2008). For example, draining wetlands in New Zealand was shown

to increase the frequency of flood peaks substantially (Jackson, 1987). A study of wetlands in Illinois estimated that as the peak-flow to average precipitation ratio decreased by (on average) 3.7%, floodflow volume to total precipitation ratio decreased by 1.4%, and low flow increased by 7.9% for an increase of one percent wetland area in a watershed (Demissie and Khan, 1993). Even beaver dams can substantially reduce discharge peaks downstream (Nyssen et al., 2011).

On the other hand, not only is there evidence that wetland drainage has little impact on flooding (e.g., Bengtson and Padmanabhan, 1999 and Ehsanzadeh et al., 2012) but also some evidence that in some circumstances, wetlands may increase flood peaks (Acreman and Holden, 2013; Brauman et al., 2007; Bullock and Acreman, 2003 and Ogawa and Male, 1986). As flood regulation relies on available water storage, permanently saturated habitats with little or no storage capacity may generate or augment floods relative to semi-saturated or unsaturated habitats (Morris and Camino, 2011). Hence, it is unclear to what extent floods are attenuated or enhanced by wetlands of different types and sizes located in areas of different topographies (Cernohous, 1979 and Smakhtin and Batchelor, 2005). This dependence of water storage capacity on wetland type and topography makes it difficult to generalize the flow regulation services of wetlands (Acreman and Holden, 2013). Bullock and Acreman (2003), in their synthesis of the hydrological functions of wetlands, concluded that although there are many qualitative assessments of the impact on flow regulation, there are few quantitative assessments.

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The flow regulation services of wetlands are of considerable interest to economists (Barbier et al., 1997; Brander et al., 2006; Brander et al., 2013; Brouwer et al., 1999; Ghermandi et al., 2010; Gren et al., 1995; Mitsch and Gosselink, 2000 and Woodward and Wui, 2001) due primarily to the health and safety hazards posed by floods and an altered flow regime (Brouwer et al., 1999; Lehner et al., 2005 and Reed and Field, 1992) and their subsequent longer-term socioeconomic consequences (Ginexi et al., 2000). Despite the perceived value and importance to humans as being one of the most productive and economically valuable ecosystems in the world, wetlands have been destroyed or degraded through activities like drainage for agriculture and industry (Millennium Ecosystem Assessment, 2005; Zedler and Kercher, 2005).

The starting point for any assessment of wetlands with respect to flow regulation services (or indeed, any ecosystem service) is an estimate of the level of service currently provided. Moreover, if biophysical, economic or socio-cultural valuations are to be used in ecosystem services assessment and decisions about ecosystem management, we must be able to estimate (with some accuracy) how the level of service provisioning is likely to change under different management scenarios.

Here we use a meta-analytic approach to evaluate the current scientific evidence concerning the flow regulation services provided by wetlands. On the basis of a comprehensive review of the published scientific literature, we address two specific questions: (1) what is the level of flow regulation services provided by wetlands as measured by effect size (an index that measures the magnitude of a treatment)? and (2) to what extent can we predict the level of flow regulation service?

Several previous meta-analyses and reviews on the ecological functions and values of wetlands (Acreman and Holden, 2013; Brander et al., 2013; Bullock and Acreman, 2003; Meli et al., 2014) provide a solid basis for the present investigation. This analysis represents an improvement in knowledge from previous meta-analyses and reviews in several ways. The broad qualitative review of Bullock and Acreman (2003) has been updated and extended by adopting a formal meta-analytic approach which permits both a quantitative estimate (effect sizes) of wetland flow regulation services as well as an examination of candidate variables (moderators) that might explain variability among studies in the estimated impact of wetlands on flow regulation. Whereas several previous meta-analyses and reviews have investigated the socio-cultural and economic value of wetlands and their provisioning of ecosystem services (see Brander et al., 2006, 2013; Brouwer et al., 1999; Ghermandi et al., 2010; Woodward and Wui, 2001) or the effects of restoration activities on biodiversity (Meli et al., 2014) and inferred ecological services, here we focus directly on flow regulation services.

## 2. Methods

### 2.1. Literature search

Literature searches were conducted in ISI Web of Science from October 2011 to May 2014. Initial searches were conducted using a combined search string with two topic fields. The first field included keywords denoting common synonyms/inflections of flow regulation (“flood control”, “flood prevention”, “flood attenuation”, “flood regulat\*”, “flood mitigation”, “flood protection”, AND “wetland\*”). The second topic field specified different wetland types (“bog”, “dambo”, “ephemeral”, “fen”, “flooded grassland\* and savanna\*”, “floodplain\* or flood-plain\*”, “marsh”, “mire”, “peat\*”, “pocosin\*”, “pond”, “pothole\*”, “paddy”, “riparian”, “swamp” and “vernal”) (step A, Appendix A, Fig. A1). Additional candidate studies were retrieved from Annex 1 of Bullock and Acreman (2003)

and by reviewing the bibliographies of all articles retrieved in step A as well as those retrieved from Bullock and Acreman (2003). Any studies that appeared to be relevant to wetland flow regulation were also included in the initial pool of candidate studies (step B-Fig. A1). Results from the initial search suggested that the set of candidate search terms in field one did not capture the full set of flow regime attributes that have been investigated by researchers. Consequently, this field was expanded to include other flow regime attributes (step C-Fig. A1) (see Appendix B for a complete list of search terms).

### 2.2. Study selection criteria

Studies examining the influence of permanent wetlands as well as floodplain and ephemeral areas that may only hold water seasonally or temporarily (i.e., not throughout the entire hydrological year) were candidates for inclusion. Studies of non-natural wetlands (e.g., paddy fields) were also potential candidates so long as impoundment or engineered flood-control structures were not part of the system.

An independent set of studies ( $k$ ) was identified based on the stringency of the applied selection criteria. In the most stringent sample, all studies retained for analysis: (i) report estimates of at least one hydrological measurement endpoint (attributes of the flow regime) or indicator (Table 1), and at least one wetland attribute (moderator) that might be expected to correlate with wetland flow (Table 2; for full description, see Appendix C) on a set of sampling units (e.g., experimental replicates, sites, etc.); (ii) provide sufficient statistical information (mean, standard deviation or some estimate of precision, correlation, sum of squares, sample size for the various groups, etc.) such that effect sizes ( $N$ ) could be estimated; (iii) included a control treatment that permitted inference about the level of flow regulation service delivered by wetlands by, for example, contrasting the level of a specific endpoint before and after wetland drainage; and (iv) were published in a peer-reviewed scientific journal or in a government/institutional report. This sample of studies was then used in a full weighted meta-analysis and meta-regression. See Appendix A for a detailed description of the study selection procedure including identification, eligibility and screening.

We also conducted separate analyses for two other different sets of studies, based on relaxation of one or more of selection

**Table 1**

Flow regulation services, associated measurement endpoints, and examples of studies that use one or more of the listed endpoints.

Flow regulation service	Measurement endpoint (units)	Example Reference
Reduction in Flooding	Average or daily discharge, flow, flood frequency, streamflow, floodflow volume to precipitation ratio, mean annual flood (Cubic meters per second ( $\text{m}^3 \text{s}^{-1}$ ), cubic feet per second ( $\text{ft}^3/\text{s}^{-1}$ ))	Wu and Johnston (2008)
	Average, maximum or instantaneous peak flow, flood peak, peak/maximum runoff, maximum flow, peak flow to precipitation ratio, peak flow ordinate, number of storm peaks above flow thresholds (Cubic meters per second ( $\text{m}^3 \text{s}^{-1}$ ), cubic feet per second ( $\text{ft}^3/\text{s}^{-1}$ ), $1 \text{ s}^{-1} \text{ ha}^{-1}$ , $1 \text{ s}^{-1} \text{ km}^{-2}$ , $\text{m}^3/\text{h}$ )	Jackson (1987)
Increase in Low Flow	Time to peak, return period, peak lag, travel time, response time of flow or runoff (days, hours, years)	Acreman et al. (2003)
Reduction in Runoff	Low Flow (Cubic meters per second ( $\text{m}^3 \text{s}^{-1}$ ), cubic feet per second ( $\text{ft}^3/\text{s}^{-1}$ ), measured at different thresholds: $Q_{75}$ , $Q_{95}$ , $Q_{99}$ , $Q_{355}$ ...)	Drayton et al. (1980)
	Average, surface or total runoff (mm, $1 \text{ s}^{-1} \text{ km}^2$ , $10^3 \text{ m}^3$ )	Jung et al. (2011)

**Table 2**  
Candidate flow regulation service moderators and associated levels.

Moderator variables	Levels
Study type	Empirical; Modelled
Wetland location	General (unknown or both headwater and floodplain); Headwater only; Floodplain only
Study design	Before-After; Before-After-Control-Impact; Control-Impact (including Correlative Designs)
Basis of inference	Based on characteristics of hydrograph river flows or river flow events of unmanipulated (undrained) systems; based on drainage
Hydrological endpoint (indicator)	Streamflow & Runoff; Peak (Flow or Time to Peak); Low Flow
Scale	Individual wetland or wetland complex; watershed/catchment

criteria (i)–(iv). A second, independent sample of studies satisfied criteria (i), (iii) and (iv) but did not provide sufficient statistical information to calculate study weights (raw differences were calculable, without estimates of precision sufficient to estimate true effect sizes). A third sample of studies included those which satisfied criteria (i), and (iv), but did not provide sufficient statistical information to estimate effect sizes or raw differences. Rather, these studies included explicit statements by the authors about the effect of wetlands on one or more endpoints. Analysis of these two samples yielded results qualitatively similar to those obtained for the full weighted meta-analysis, and hence, are not reported here.

For a complete list of the articles included in the weighted meta-analysis dataset, see [Appendix E](#).

### 2.3. Estimation of flow regulation services

We considered a wetland to provide some level of flow regulation service if, in comparison to an appropriate “reference” situation (e.g., presence versus absence of a wetland or wetland complex; flow entering or exiting a wetland or wetland complex; drained versus undrained wetland(s), etc.): there were differences in peak flows or floodflows (frequency, timing or magnitude), low flows, runoff or streamflow, all of which are implicated in the flow regulation services attributed to wetlands ([Bullock and Acreman, 2003](#); [Demissie and Khan, 1993](#) and [Mitsch and Gosselink, 2007](#)). To each of these attributes of the flow regime correspond one or more hydrological endpoints ([Table 1](#)), the level of which can be compared between reference and treatment conditions. Differences were considered to indicate flow regulation service provisioning by wetlands if, relative to the reference situation, treatments showed (i) reduced flooding (as measured by peak flow or floodflow); (ii) increased time to peak; (iii) augmented low flows; or (iv) reduced runoff (the flow [discharge of seepage] of water over land that occurs when the soil has reached its infiltration capacity) or general streamflow (the flow [discharge-volume rate] of water flowing in a channel). In a meta-analytic approach, these differences are quantified as effect sizes, with each study contributing one or more effect size estimates. In some cases, studies contributed multiple effect sizes to the sample, with different effect sizes corresponding to different hydrological endpoints (e.g., a study which examined both peak flow and low flow might contribute two or more effect size estimates).

We also sought to explain variability among studies in estimated flow regulation services by identifying a set of candidate moderators about which information was available for most of the studies satisfying our inclusion criteria. These variables include two broad classes ([Table 2](#)): (a) attributes of the study design (e.g., which hydrological endpoints were employed, whether the study was an empirical or modelling study) ([Leuzinger et al., 2011](#)),

study design (before-after, control-impact, and before-after-control-impact studies) ([Carlson and Schmidt, 1999](#)), geographical scale (watershed versus individual wetland(s)), and whether the study involved inference of flow regulation services based on hydrographs of river flow events of undrained systems versus inferences based on a comparison of drained and undrained wetlands (basis of inference); (b) attributes of the wetland, wetland complex or landscape under investigation, for which there is empirical evidence of an association with flow regulation services (e.g., wetland location ([Bullock and Acreman, 2003](#))). We examined the association between these candidate moderators and study effect sizes using meta-regression ([Borenstein et al., 2009](#); see [Section 2.5](#) below).

### 2.4. Study design and effect size estimation

Studies on wetland flow regulation services span a wide range of designs, including Before/After (BA) designs; Control-Impact (CI) designs, which include Simple Treatment-Control (sTC) as well as Multiple Treatment-Control (mTC) designs; Correlative Designs (CD), both simple (sCD) and multiple (mCD); and Before/After-Control/Impact (BACI) designs. The appropriate effect size measure depends on the study design. For BA, sTC and BACI designs, raw effect sizes (Cohen's  $d$ ) were calculated based on the standardized mean difference between appropriate conditions (e.g., in BA designs, before and after wetland drainage). For mTC and mCD designs  $\eta^2$  was used as the raw measure of effect. This effect size measure is analogous to the coefficient of determination ( $r^2$ ) but is used for designs that compare more than two groups. For sCD designs, the Pearson correlation coefficient ( $r$ ) was used as the raw effect size measure. For a full explanation of different study designs and their associated effect size measures, see [Appendix D](#).

### 2.5. Weighted meta-analysis

Weighted meta-analysis was performed as described by [Borenstein et al. \(2009\)](#), [Harrison \(2011\)](#) using a random effects model that assumes that the true effect size varies among studies. All raw effect sizes (standardized mean difference between groups (Cohen's  $d$ ), correlation coefficients ( $r$ ) or  $\eta^2$ ), as described above) were converted to correlation coefficients, thence to Fisher's  $z$  scale (an approximate variance-stabilizing transformation) as the principal effect size measure of interest ([Borenstein et al., 2009](#)). For presentation purposes, effect sizes have been reconverted to correlation coefficients.

We used mixed-effects meta-regression to examine the association between effect size and candidate moderator variables using the Empirical Bayes method (one of several possible estimators) to estimate heterogeneity ( $\tau^2$ ) ([Morris, 1983](#) and [Raudenbush and Bryk, 1985](#); see also [Viechtbauer, 2010](#)). Meta-regression analysis was conducted using the metafor package ([Viechtbauer, 2010](#)) in R version 2.13.2 ([R Development Core Team, 2011](#)). Fitted models were evaluated on the basis of Akaike Information Criterion (AIC) and analog  $R^2$ , both of which provide information on model fit and allow direct comparison among fitted models, accompanied by corresponding QE (test statistic of residual heterogeneity) and QM (Omnibus test statistic of moderators). Given the limitations of comparatively small number of effect sizes ( $N$ ), we restricted the number of fitted parameters ( $p$ ) in any candidate model such that the  $N/p$  ratio was greater than 5, sufficient – at least in principle – to ensure reasonable model stability and/or sufficient precision of estimated coefficients ([Vittinghoff et al., 2005](#)).

On the basis of fitted meta-regression models, we estimated the predictive value of candidate moderators, or sets thereof, with

respect to observed effect sizes using analog  $R^2$  as a measure of predictive power. Heterogeneity was assessed using weighted sum of squares (Q); tau-squared ( $\tau^2$ ) (estimate of between-studies variance); the proportion of observed variance that reflects real differences in effect size ( $I^2$ ); and the ratio of total variability to sampling variability ( $H^2$ ).

Publication bias occurs when studies that report relatively high effect sizes are more likely to be published than studies that report lower effect sizes. To explore potential agenda-driven and publication biases in the set of selected studies, we used funnel plots (Borenstein et al., 2009) and fail-safe  $N$  (Rosenberg, 2005; Rosenthal, 1979).

As noted above, many studies generated multiple effect sizes corresponding to different hydrological endpoints. This introduces two potential problems: (1) the standard summary effect treats each effect size as an observation, thereby giving studies with multiple estimates more weight in the analysis; and (2) the analysis ignores the possibility of within-study correlations among effect size estimates, potentially leading to an overestimated precision of the summary effect (Borenstein et al., 2009). To address this potential bias, we calculated the intra-class correlation (ICC) based on the within- and between-study variances in effect size for all studies with multiple effect sizes. We then calculated a synthetic effect size for each study defined as the mean effect size in the study based on all endpoints, as well as a synthetic within-study variance based on the ICC using Eq. (5) of Borenstein et al. (2009, pp. 228). Meta-regression models were then fit to examine associations between synthetic effect size and candidate moderators at the study level.

### 3. Results

Initial screening retrieved 361 articles, of which 237 failed to satisfy the inclusion criteria (step D–Fig. A1). Ninety-six of the remaining 124 candidate studies were excluded from weighted meta-analysis because (a) no online or print versions were available (this was the case for many U.S. Geological Survey [USGS] sources) or only an abstract was available (23 studies, step E–Fig. A1); or (b) inadequate study design or insufficient statistical data to estimate effect sizes (73 studies, step F– Fig. A1). In total, 28 studies and 59 effect sizes were included in weighted meta-analysis of which, 24 (86%) came from peer-reviewed literature and 4 (14%) from institutional reports.

#### 3.1. Weighted meta-analysis

Fifty-nine weighted effect sizes were calculated from the 28 studies, yielding a medium positive mean effect size of  $0.52 \pm 0.10$  (one standard error (SE)),  $k=28$ ,  $N=59$ ,  $p < 0.0001$ , 95% CI=[0.32, 0.71], corresponding to a weighted overall mean correlation coefficient ( $r$ ) of 0.47 based on z-transformed values of 0.52. Two estimated effect sizes (3% of the data set) from two separate studies were negative. All five measures of heterogeneity indicated substantial variation in effect size among studies (Q Test for Heterogeneity=8750,  $df=58$ ,  $p < 0.0001$ ;  $\tau^2=0.54$ ; T standard deviation of underlying effects across studies=0.73;  $I^2=98.9\%$ ;  $H^2=93.8$ ).

Effect sizes showed an informative bivariate association with study type (empirical ( $N=35$ ) versus modelled ( $N=24$ )) (AIC (null)=142.4; AIC (model)=136.61; analog  $R^2=0.12$ ) with empirical studies having, on average, smaller effect sizes than hydrological modelling studies (Fig. 1a). Because of this difference, and because the distribution of other candidate moderator variables differed dramatically between empirical and modelling studies, we subsequently conducted meta-regression analysis for empirical and modelling studies separately.

Thirty-five effect sizes were calculated from 17 empirical studies. Weighted meta-analysis yielded a small positive overall mean effect size of  $0.28 \pm 0.06$  (1 SE), 95% CI=[0.16, 0.41], corresponding to a weighted overall mean correlation coefficient ( $r$ ) of 0.28 based upon z-transformed values of 0.28, with moderate heterogeneity ( $\tau^2=0.11$ ). Four moderators showed informative bivariate associations with study effect size: study design (Fig. 1b; BA ( $N=3$ ), CI ( $N=24$ ), BACI ( $N=8$ )); hydrological endpoint (Fig. 1c; Streamflow & Runoff ( $N=12$ ), Peak ( $N=19$ ), Low Flow ( $N=4$ )); basis of inference (Fig. 1d; Hydrograph ( $N=20$ ), Drainage ( $N=15$ )); and scale (Fig. 1e; Wetland ( $N=23$ ), Watershed ( $N=12$ )) (Table 3). On the basis of this analysis then, larger estimates of flow regulation services are associated with before-after study designs compared to control-impact designs; with peak (time and flow) compared to low flow; with estimates based on drainage studies compared to inference of flow regulation services based on hydrographs of river flows or river flow events in undrained systems; and with studies at the individual wetland or wetland complex scale compared to the drainage basin scale. There was support for only one multivariable model, that which included both study design and hydrological endpoint as informative moderators. However, this model was only marginally more informative than the best univariate models.

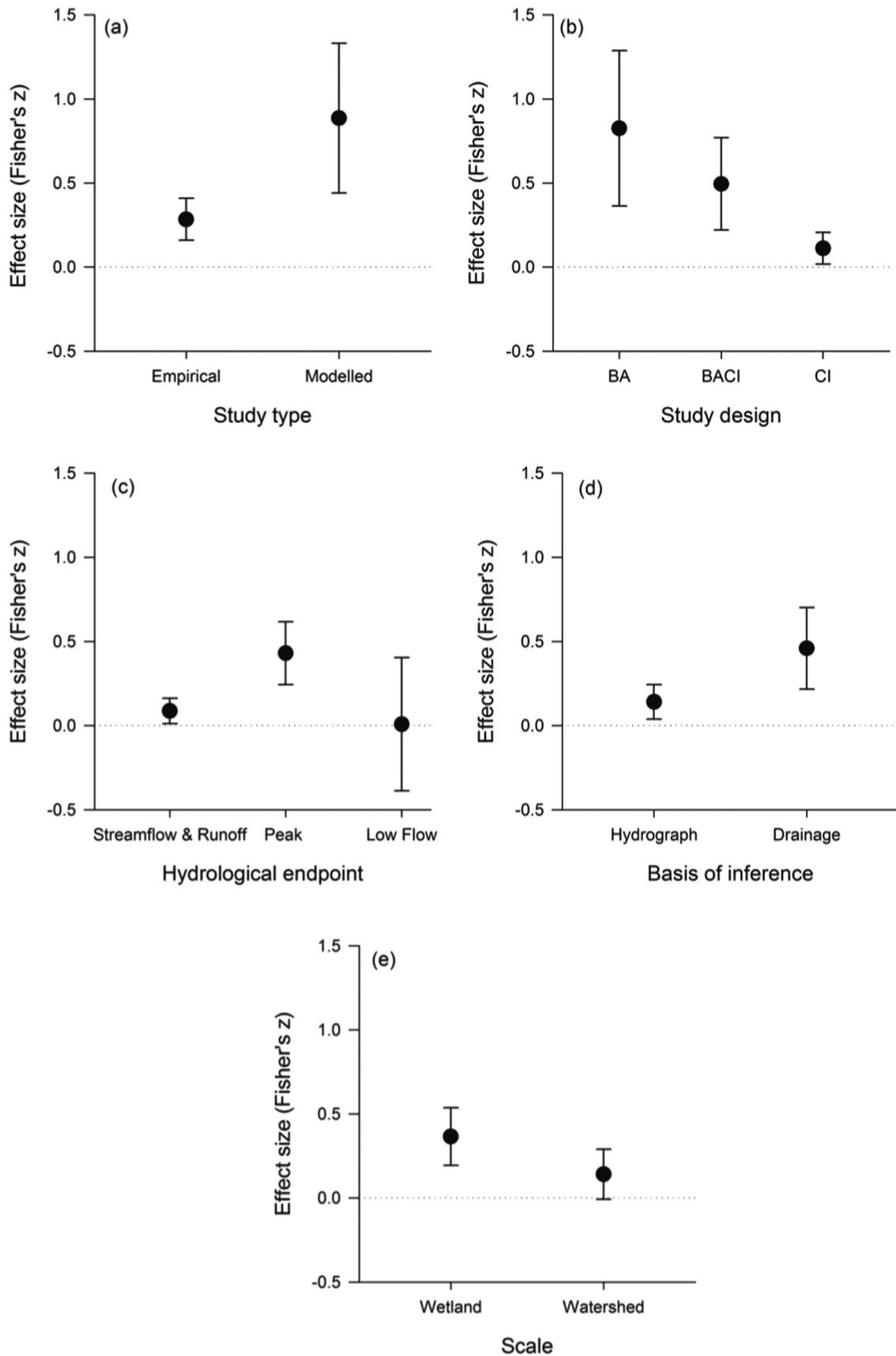
Twenty-four effect sizes were calculated from 11 modelled studies. Weighted meta-analysis yielded a large positive overall mean effect size of  $0.89 \pm 0.23$  (1 SE) (Fig. 1a), 95% CI=[0.44, 1.33], corresponding to a weighted overall mean correlation coefficient ( $r$ ) of 0.71 based upon z-transformed values of 0.89, with substantial heterogeneity ( $\tau^2=1.13$ ).

All of the candidate moderator variables that showed detectable associations with effect sizes of empirical studies showed insufficient variation in the subset of modelled studies to permit analysis of potential associations (Table E1, Appendix E). Consequently, we compared moderator variable results among two different analyses: weighted meta-analysis of individual empirical effect sizes (results presented above); and weighted meta-analysis of synthetic empirical effect sizes (Table E1).

#### 3.2. Meta-analysis of synthetic effect sizes

For both empirical and modelling studies, there was strong correlation among endpoint effect sizes within studies (ICC=0.85) (Fig. E1). Weighted meta-analysis of synthetic effect sizes yielded a moderate positive mean effect size of  $0.52 \pm 0.14$  (1 SE),  $k=N=28$ ,  $p < 0.0001$ , 95% CI=[0.25, 0.79], corresponding to a weighted overall mean correlation coefficient ( $r$ ) of 0.48 based upon z-transformed values of 0.52. For the subset of  $k=N=17$  empirical studies, ICC=0.84 (Table F2). Weighted meta-analysis of synthetic empirical effect yielded a moderate positive mean synthetic effect size  $0.32 \pm 0.09$  (1 SE),  $p=0.0004$ , 95% CI=[0.14, 0.49], corresponding to a weighted overall mean correlation coefficient ( $r$ ) of 0.31 based upon z-transformed values of 0.32.

Meta-regression results for synthetic empirical effect size are consistent with the initial weighted analysis. Three moderators showed informative bivariate associations with synthetic effect size: study design (Fig. 2a; BA ( $N=2$ ), CI ( $N=10$ ), BACI ( $N=5$ )); basis of inference (Fig. 2b; Hydrograph ( $N=9$ ), Drainage ( $N=8$ )); and scale (Fig. 2c; Wetland ( $N=13$ ), Watershed ( $N=4$ )) (Table 3). As was the case for the weighted meta-regression, larger synthetic effect sizes were associated with before-after designs compared to control-impact designs; studies for which estimates were based on drainage versus inferences based on hydrographs of river flows or river flow events in undrained systems; and with studies focused on the individual wetland or wetland complex scale compared to the drainage basin scale. There was no support for any multivariable models: all candidate multivariate models either resulted



**Fig. 1.** Mean effect sizes and associated 95% confidence intervals for all moderators (variables) showing informative bivariate associations with effect size in the full ( $k=28$ ,  $N=59$ ) set of studies included in weighted meta-analysis (a), and the subsample of empirical ( $k=17$ ,  $N=35$ ); studies (b–e): (a) study type; (b) study design (BA=Before-After, BACI=Before-After-Control-Impact, CI=Control-Impact); (c) hydrological endpoint; (d) basis of inference; and (e) spatial scale. For more details, see text.

**Table 3**

Moderators showing bivariate associations with effect sizes of empirical studies ( $k=17$ ,  $N=35$ ) and empirical synthetic effect sizes ( $k=N=17$ ) in fitted bivariate models. For the full set of empirical studies, only one multiple variable model was only marginally more informative than the best bivariate model. For empirical synthetic effect sizes, no candidate multivariable model was more informative than the best univariate model.

Moderator (s)	AIC	Analog $R^2$	QE	QM
Null model (Empirical studies)	37.8	–	–	–
Study design	24.2	0.48	100.53 ( $p < 0.0001$ )	34.69 ( $p < 0.0001$ )
Hydrological endpoint	34.7	0.18	197.12 ( $p < 0.0001$ )	7.87 ( $p=0.02$ )
Basis of inference	34.9	0.14	308.36 ( $p < 0.0001$ )	5.32 ( $p=0.02$ )
Scale	37.2	0.06	309.03 ( $p < 0.0001$ )	2.65 ( $p=0.1$ )
Study design+Hydrological endpoint	24.8	0.51	86.09 ( $p < 0.0001$ )	28.22 ( $p < 0.0001$ )
Null model (Empirical synthetic effect sizes)	20.3	–	–	–
Study design	13.7	0.56	44.64 ( $p < 0.0001$ )	14.28 ( $p=0.0008$ )
Basis of inference	18.1	0.25	97.98 ( $p < 0.0001$ )	4.75 ( $p=0.03$ )
Scale	19.8	0.12	98.04 ( $p < 0.0001$ )	2.61 ( $p=0.11$ )

in  $N/p$  ratios too small to have much confidence in estimated coefficients, or were only marginally more informative than the corresponding univariate models.

Synthetic effect size analysis was also carried out on the subset of modelling studies ( $k=N=11$ ), yielding an ICC of 0.88 based on a synthetic effect size (Fisher's  $z$ -transformed correlation coefficient) (Table F2). The resulting weighted meta-analysis yielded an overall mean effect size of  $0.87 \pm 0.32$  (1 SE),  $p=0.007$ , 95% CI = [0.24, 1.5], corresponding to a weighted overall mean correlation coefficient ( $r$ ) of 0.7 based upon  $z$ -transformed values of 0.87.

### 3.3. Publication bias

The funnel plot (Fig. F2), which describes the relationship between individual effect size estimates and the associated standard error of the effect size, suggests little publication bias i.e., no detectable pattern or asymmetry (see Borenstein et al., 2009) but substantial variation in effect sizes among studies. A formal test for funnel plot asymmetry, based on the random-effect regression (regression test, Egger et al., 1997) indicates some asymmetry between observed outcomes and chosen moderator-standard error ( $z = -3.1$ ,  $p=0.002$ ).

Duval and Tweedie's (2000a, 2000b) "trim-and-fill" procedure removes the most extreme small studies from the positive side of the funnel plot and re-computes the effect size at each iteration until the funnel plot is symmetric, thereby generating an unbiased effect size estimate. Using this method, the estimated number of missing studies on the left side of the funnel plot is zero, suggesting that our estimated overall effect size is unaffected by bias.

### 3.4. Fail-safe $N$

We can compute how many missing studies we would need to retrieve and incorporate in the analysis before the estimated overall effect is eliminated. Rosenthal's (1979) Fail-safe  $N$  (8287 studies–Observed Significance Level:  $< 0.0001$ , Target Significance Level=0.05), as well as Rosenberg's (2005) Fail-Safe  $N$  (6458 studies; observed significance level  $< 0.0001$ , target significance level=0.05), both suggest little reason for concern, as a large

number of contradictory studies would be required to overcome the observed positive effect.

## 4. Discussion

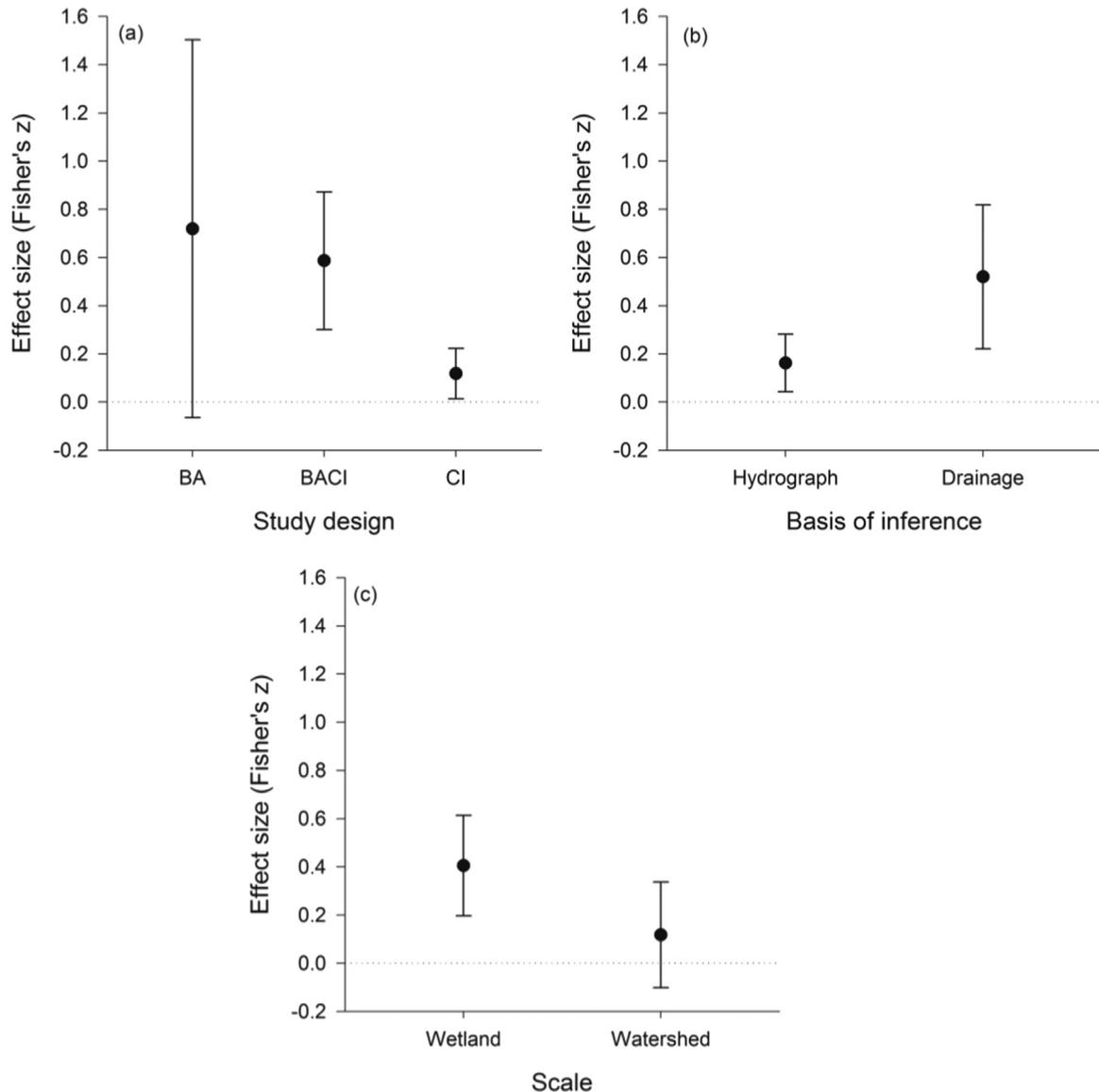
A comprehensive search of the literature on wetland flow regulation services turned up comparatively few ( $N=28$ ) studies that satisfied our inclusion criteria for weighted meta-analysis. The associated comparatively small sample ( $k=59$ ) of associated effect sizes limits our ability to explore and test possible associations with candidate moderator variables and, in particular, the fitting of multivariable models, especially when synthetic effect sizes is the response variable of interest. On the other hand, relaxation of several relaxation criteria generated independent sets of studies (and associated effect sizes), analysis of which indicated patterns and associations qualitatively similar to those reported here. We are, therefore, cautiously optimistic that these associations will be reproducible and robust.

Our results provide evidence that, on average, wetlands deliver significant positive flow regulation services corresponding to reduced frequency and magnitude of flooding, increased flooding return period, augmented low flows, and reduced streamflow and runoff. However, there was substantial variation in the estimated level of service among studies, with some (3%) documenting negligible or even negative effects (e.g., decreased peak flows after wetland drainage, Lundin, 1994).

Meta-regression (prediction) analysis indicates that the magnitude of the estimated wetland effect on flow regimes (i.e., effect size) depends on study type and design. The estimated effect of wetlands on flow regulation services was, on average, larger for modelling studies than empirical studies. Results of modelling studies are not only susceptible to uncertainty in parameter estimates, but also more fundamental uncertainty associated with the degree to which any model fully captures underlying processes. In modelling, the focus will inevitably be on those processes regarded as being better understood. The result may well be that the effects of known processes are exaggerated. Certainly those involved in modelling wetland functions admit that their predictive power is poor (see, e.g. Batker et al., 2010; Yang et al., 2010).

Larger average flow regulation services were also associated with before-after (BA) study designs, with control-impact (CI) designs having the smallest average effect sizes. The association between attributes of the study design and estimated effect sizes has been noted previously (e.g., Balvanera et al., 2006; Lepš, 2004; Schmid et al., 2002). For example, in a recent meta-analysis Meli et al. (2014) found that the estimated effects of wetland restoration depended both on which attributes were assessed and the experimental design, with Before-After (BA) restoration experiments associated with an estimated 33% increase in biodiversity and ecosystem services compared to a 22% increase for Control-Impact (CI) studies. The larger effect sizes associated with BA studies may be a result of their tendency to overestimate the effects of interventions (e.g., Gelman, 2004; Grimshaw et al., 2000; Meli et al., 2014) owing to the confounding of natural versus intervention-induced changes, or because the design largely eliminates the (often large) spatial variability in ecological processes present in CI designs.

Differences were also detected among different hydrological endpoints, with peak and runoff/streamflow showing the largest average effect sizes, low flow the smallest; suggesting that wetlands have larger flood and streamflow mitigation effects than low flow augmentation effects. However, these differences may have less to do with hydrological reality and more to do with the lack of a systematic characterization and definition of the hydrological properties/processes of concern, and (more especially), how to



**Fig. 2.** Mean effect sizes and associated 95% confidence intervals for all variables showing informative bivariate associations with synthetic empirical effect size ( $k=N=17$ ): (a) study design (BA=Before-After, BACI=Before-After-Control-Impact, CI=Control-Impact); (b) basis of inference; and (c) spatial scale. For more details, see text.

about estimating them. For example, [Bullock and Acreman \(2003, p. 362\)](#) note that “published studies in wetland hydrology are not consistent in their attention to different measures; it is possible to find one study analysing the return period of flood peaks extracted from a 20 or 30 year flow records, and another analysing the flood volume of a single event, with both drawing conclusions on wetland influences on floods”. In particular, low-flow analysis employs flow duration curves that require investigators to select specific low-flow parameters that can vary substantially among studies. Such between-study variation in low-flow characterization may well explain the comparatively smaller average weighted effect size reported here. On the other hand, differences in average effect sizes among hydrological endpoints may also reflect real differences in sensitivity of different attributes of the flow regime to local conditions. For example, there is evidence that under certain circumstances, wetlands may reduce low flow ([Bullock, 1992](#); [Drayton et al., 1980](#) and [Riddell et al., 2013](#)), under other conditions increase it ([Ahmed, 2014](#); [Bullock and Acreman, 2003](#) and [Demissie and Khan, 1993](#)).

We also found that studies that involved a single wetland or wetland complex had, on average, larger associated effect sizes

than studies at the watershed or drainage basin scale. Hydrological services estimated at broader spatial scales will be less influenced by individual wetland properties simply because of the broader influence, at this scale, of other factors, including land cover, surficial geology, and topography. It is well-understood, for example, that other types of natural land cover can absorb flood waters, though perhaps less effectively than wetlands ([Boyd and Wainger, 2003](#)). Because at local scales, the variability in (and hence, the statistical noise arising from) these factors is smaller, the effect of wetlands per se is likely to be more easily detected.

Some of the observed variation among studies in estimated effect sizes reflects apparent differences in the effects of wetland drainage. Larger estimates of flow regulation services were, on average, associated with estimates based on drained and undrained wetlands studies compared to inference of flow regulation services based on hydrographs of river flows or river flow events in undrained wetland systems. The literature includes examples where drainage has resulted in increased peak flows ([Ballard et al., 2012](#); [Irwin and Whiteley, 1983](#); [Robinson, 1990a](#)), others where it has led to reduced peak flows ([Irwin and Whiteley, 1983](#); [Robinson, 1990a](#)). Similarly, some studies have concluded draining

wetlands contributes more to streamflow than undrained wetlands (Jackson, 1987; Malcolm, 1979; Robinson, 1986, 1990b), while other studies have demonstrated drainage leading to reduced flows (Baden and Eggelsmann, 1970; Lundin, 1994; Newson and Robinson, 1983).

One possible explanation for the observed variation in the effects of wetland drainage may relate to wetland location. Upstream wetlands are likely better suited to immediately (but temporarily) store floodwaters compared to downstream wetlands that are less likely to be saturated. But due to their upstream position, they may also be more prone to releasing stored floodwaters downstream. If so, drained upstream or head water wetlands will be more likely to increase flow rates, thus leading to events that contribute to flooding further downstream. On the other hand, drainage of downstream wetlands - which may already be saturated with water from upstream sources - may provide more consistent short-long term flood water storage capacity. Reduction in flood flows after drainage may be due to progressive changes in peat/soil compressibility after drainage; an increase in storage capacity of the soil layer due to groundwater table decline (loss of flow/runoff); reduction in hydraulic conductivity; and increased evaporation related to changes in vegetation/land cover (Holden et al., 2004; Katimon et al., 2013).

The ecosystem service approach, as originally proposed (Costanza and Daly, 1992; Costanza et al., 1997; Perrings et al., 1992) requires translating knowledge about ecosystem services into policy and decision-making tools. The problem, however, is not simply that ecosystem services are undervalued (Costanza et al., 1997; Postel and Thompson, 2005), but that they are poorly characterized and poorly understood scientifically (Chan et al., 2006; Kremen, 2005; Wallace, 2007). The process of bridging the gaps between the natural and social sciences through the ecosystem services concept and agenda must include knowledge of the ecological systems (i.e., ecosystem function; ecological structures and processes) that provide the services (Braat and de Groot, 2012). In Daily et al.'s (2009) words, "In promising a return (of services) on investments in nature, the environmental scientific community needs to deliver the knowledge and tools necessary to forecast and quantify this return" (p. 21). In other words, to be of practical utility in decision-making, it must be capable of estimating - with reasonable accuracy and precision - the level of service currently being delivered under different management regimes.

In this context, our results have several implications. First, our results add biophysical evidence to a growing body of meta-analytic investigations and reviews (e.g., Brander et al., 2006, 2013; Brouwer et al., 1999; Bullock and Acreman, 2003; Ghermandi et al., 2010; Meli et al., 2014; Woodward and Wui, 2001) that suggest a positive effect of wetlands on flow regulation services. This implies that degradation of wetlands is likely to reduce the flow regulation services from which humans currently benefit. Maintaining such services then depends on either reversing general trends of wetland loss and degradation, or adopting appropriate - but almost certainly more costly - compensation strategies (Juliano, 1999).

Second, our results also indicate that our ability to predict the level of flow regulation service delivery based on information that might be generally available, is modest at best. This, combined with the observed large variation in estimated effect sizes, means that, in the absence of considerably more detailed in situ information, any estimate of the current level of flow regulation service delivered by a wetland, or the expected change in service provisioning under alternative management actions, will have a correspondingly large associated uncertainty. As such, ascribing general flow regulation functions and services to specific wetlands or wetland complexes of management interest is probably unjustified (Ahmed, 2014; Bullock and Acreman, 2003; Staes et al., 2009).

There is already a vigorous debate among ecological economists about appropriate methodologies for estimating the economic value of ecosystem services, especially those for which no market exists (see e.g., Bockstael et al., 2000; Howarth and Farber, 2002; Wilson and Carpenter, 1999). Moreover, even estimates of the economic value of flow regulation services of wetlands are highly variable (Gren et al., 1995; Woodward and Wui, 2001) depending on factors such as wetland productivity (Costanza et al., 1989), the valuation method employed (Lambert, 2003), and wetland location (Mitsch and Gosselink, 2000). To these methodological limitations must now be added the arguably even more fundamental constraint that, in the absence of detailed hydrological and ecological information, we have limited ability to predict the level of flow regulation service currently provided by a wetland or wetland complex. The implication is that in the absence of detailed biophysical information, any quantitative estimate of the economic value of ecological service provisioning may have such large associated uncertainty as to be of limited value. This conclusion, for what appears as one of the most intensively studied combination of ecosystems (wetlands) and services (flow regulation), does not bode well for the many other ecosystems and services that are more poorly studied but for which a quantitative evaluation of ecosystem service provisioning under different management regimes is sought.

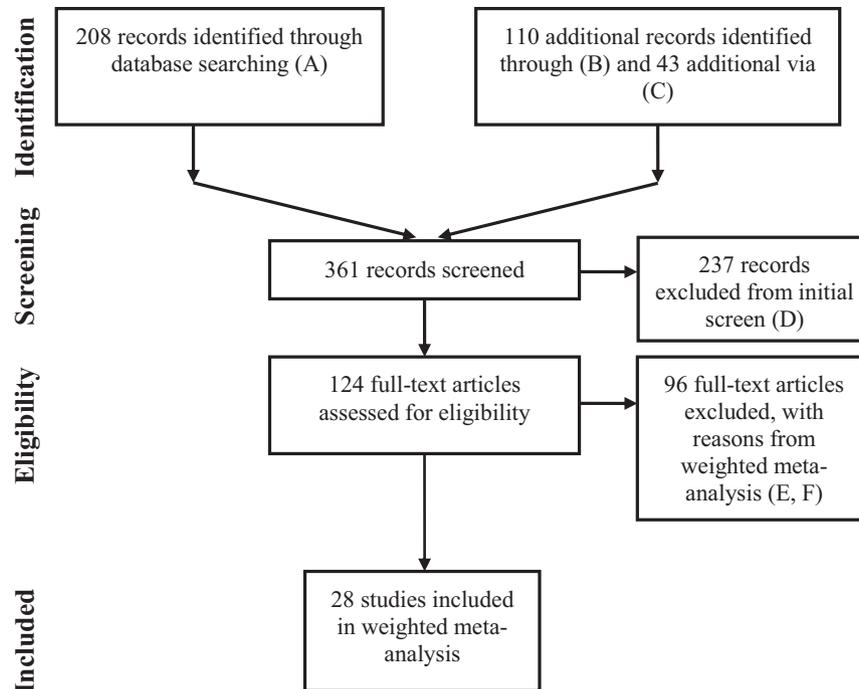
On the other hand, even highly uncertain estimates of ecosystem services can be employed to test hypotheses concerning the impacts of human activities on ecosystem services; identify stakeholders affected by land use decisions which might be expected to affect ecosystem services provisioning; identify the significance of ecosystem services benefits through socio-cultural and economic valuation; and perhaps most importantly, be used as a decision-support tool/method to integrate and analyze results, implications, and trade-offs for ecosystem services management. We caution, however, that all such analyses should explicitly both incorporate and confront the (in our view, inevitable) large uncertainty associated with estimates of current ecosystem service delivery as well as expected changes therein under alternate management scenarios.

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## Appendix A. Flow chart and study selection procedure

Step A-initial search query using a combined search of flow regulation synonyms and different wetland types in ISI Web of Science [see Section 2.1 of the main text]; Step B-studies retrieved using Annex 1 of Bullock and Acreman (2003) and by reviewing bibliographies of articles retrieved in Step A; Step C-secondary search queries using additional search terms and phrases that were not included in step A, but which were prevalent in abstracts of articles retrieved in steps A and B [see Appendix B]; Step D-study exclusion based on failure to satisfy one or more inclusion criteria; Step E- exclusion from weighted meta-analysis owing to



**Fig. A1.** Flow chart of study identification from a literature search and screening eligibility based on appropriate inclusion criteria .

absence of online or print version of full article; Step F-exclusion from weighted meta-analysis owing to inadequate study design or insufficient statistical data to estimate effect sizes. Fig. A1.

#### Appendix B. Additional search terms and phrases used in study searches

Each search in ISI Web of Science combined a primary and secondary search string.

##### Primary search strings.

“after drain\*”, “allevia\*”, “attenua\*”, “beaver”, “discharge”, “drain\* after”, “draining”, “drained”, “drainage”, “effect of”, “effect\* hydrology”, “flood”, “floods”, “flooding”, “flow regime”, “function”, “functions”, “functioning”, “hydrolog\* effect”, “hydrolog\* impact\*”, “hydrologic\* process”, “influence of”, “impact of”, “impacts of drainage”, “low flow”, “low-flow”, “model\* flood\*”, “model\* the flood\*”, “optimum”, “peak flow”, “reclamation”, “restoration”, “retard\*”, “river flood”, “river flow\*”, “riverflood”, “role of”, “runoff”, “run-off”, “simula\* flood\*”, “simula\* the flood\*”, “stream flood”, “stream flow”, “streamflood”, “streamflow”, “stormflow”, “time to peak”, “time-to-peak”, “water budget”, “water storage”, “water-storage”, “wetland flow”, and “wetland storage”.

##### Secondary search strings.

“bog”, “dambo”, “ephemeral”, “fen”, “flooded grassland\* and savanna\*”, “floodplain\* or flood-plain\*”, “marsh”, “mire”, “peat\*”, “pocosin\*”, “pond”, “pothole\*”, “paddy”, “riparian”, “swamp” and “vernal”.

#### Appendix C. Description of candidate moderators

We constructed a database similar in structure to that developed by Bullock and Acreman (2003), in which records are studies,

with multiple records per study in cases where multiple endpoints were estimated. For each study we extracted information to calculate effect sizes, as well as information on a set of potential moderator variables that might be associated with the delivery of wetland flow regulating ecosystem services. The candidate moderators are described in Table C1.

*Study type:* An ‘Empirical’ study is one in which the flow regime of wetlands were measured or estimated in the field. A ‘Modelled’ study refers to one in which the effect of wetland(s) was inferred based on some sort of model, often a simulation model. In such studies, model parameters – if estimated empirically – were not based on measurements of a specific wetland or wetland complex.

*Study design:* Studies on wetland flow regulation services span a wide range of approaches and methodologies. Studies were classified based on several different attributes: (1) empirical versus modelling studies; and (2) study design, including Before/After (BA), Control-Impact (CI- includes: Simple Treatment-Control (sTC), Multiple Treatment-Control (mTC)), simple Correlative Design (sCD), Multiple Correlative Design (mCD)), and Before/After-Control/Impact (BACI) designs. For more detail on study designs and calculation of associated effect sizes see Appendix D.

*Wetland location:* A ‘headwater’ wetland is any wetland that is not a floodplain. A ‘floodplain’ is a flat or nearly flat surface of land neighbouring a stream or river and usually does not store water year round unless it experiences high periods of flooding or discharge.

*Basis of inference:* This variable describes how wetland flow regulation services were inferred. Some studies inferred wetland services based on the characteristics of the hydrograph of river flows or river flow events in unmanipulated (undrained) systems, while others inferred wetland function by contrasting drained and undrained systems.

*Hydrological endpoints (indicators):* Hydrological endpoints included ‘Streamflow’, volume per unit time (discharge) of water flow through a channel (streams, rivers, delta, straits etc.); ‘Runoff’, the flow that occurs when the soil has reached saturation

**Table C1**

Candidate flow regulation service moderators, associated levels and coding. (Table 2 in the main text also provides a list of candidate predictor variables used in this study).

Study Type	Empirical	0	Modelled	1		
Study Design	Before-After	0	Before-After- Control- Impact	1	Control-Im- pact (Correlat- ive included)	2
Wetland Location	General (unknown or both headwater and floodplain)	0	Headwater	1	Floodplain	
Basis of Inference	Based on character- istics of hydrograph river flows or river flow events of un- manipulated systems	0	Drainage	1		
Hydrological Endpoint (indicator)	Streamflow and Runoff	0	Peak (Flow and Time to Peak)	1	Low Flow	2
Scale	Individual wetland or wetland complex	0	Watershed/ Catchment	1		

**Table D1**

The effect size measure employed for different flow regulation service study designs.

Effect size basis	Study design	Study type	Effect size measure	Reference examples
Effect size based on correlation	Simple Correlat- ive Design	Empirical and Modelled	Correlation coefficient ( $r$ )	Bullock (1992), Demissie and Khan (1993), Ogawa and Male (1986)
Effect size based on two means	Before-After; Simple Treat- ment-Control; Before/After- Control/ Impact	Empirical and Modelled	Standardized mean difference (Cohen's $d$ )	Balek and Perry (1973), Lundin (1994), Smakhtin and Batchelor (2005)
Effect size based on more than two means	Multiple Treatment- Control; Multiple Correlat- ive Design	Empirical and Modelled	Eta-squared ( $\eta^2$ )	Jung et al. (2011), Martinez-Martinez et al. (2014), Vinning (1998)

(overland flow, surface runoff); 'Peak Flow', the peak flow of discharge during a hydro-period; 'Time to Peak', the time from return of flood or time from onset to peak of flood; and 'Low Flow', the lowest (minimum) sustained flow over a hydro-period.

*Scale:* Studies conducted at the 'wetland' scale were those involving a single, paired or multiple characterized wetland units in a local area. 'Watershed' scale studies evaluated the influence of wetlands at the scale of an entire drainage basin or catchment.

#### Appendix D. Study designs and calculation of effect sizes

Table D1. summarizes the effect size calculations for different study designs. For Before-After (BA) designs, one or more hydrological endpoints were measured/estimated for one or more sampling units (e.g., wetlands) before and after an intervention (e.g., drainage). Effect sizes were calculated based on the standardized mean difference (averaged over sampling units) of the endpoints before and after intervention (e.g., average peak flow, before and after drainage – see, for example, Lundin, 1994).

Control-Impact studies comprise several different study designs, all of which are generalizations of a Treatment-Control (TC) study replicated in various ways. We distinguished two types of TC designs. Simple (sTC) designs involve two groups of observations of one or more hydrological endpoints: those associated with a reference (control) situation (e.g., a natural unmodified wetland), and those associated with a single treatment (e.g., a modified wetland). As in BA studies, effect sizes were calculated as the standardized mean difference between the treatment and control cases (e.g., simulated flows in a catchment with and without the presence of a wetland - Smakhtin and Batchelor (2005)). By contrast, certain (rare) study designs required a comparison among more than two groups (multiple - mTC). For example, Vinning (1998) reported the results of a study in the Starkweather Coulee subbasin, North Dakota where streamflow was simulated for various open wetlands (treatments) using six separate groups of

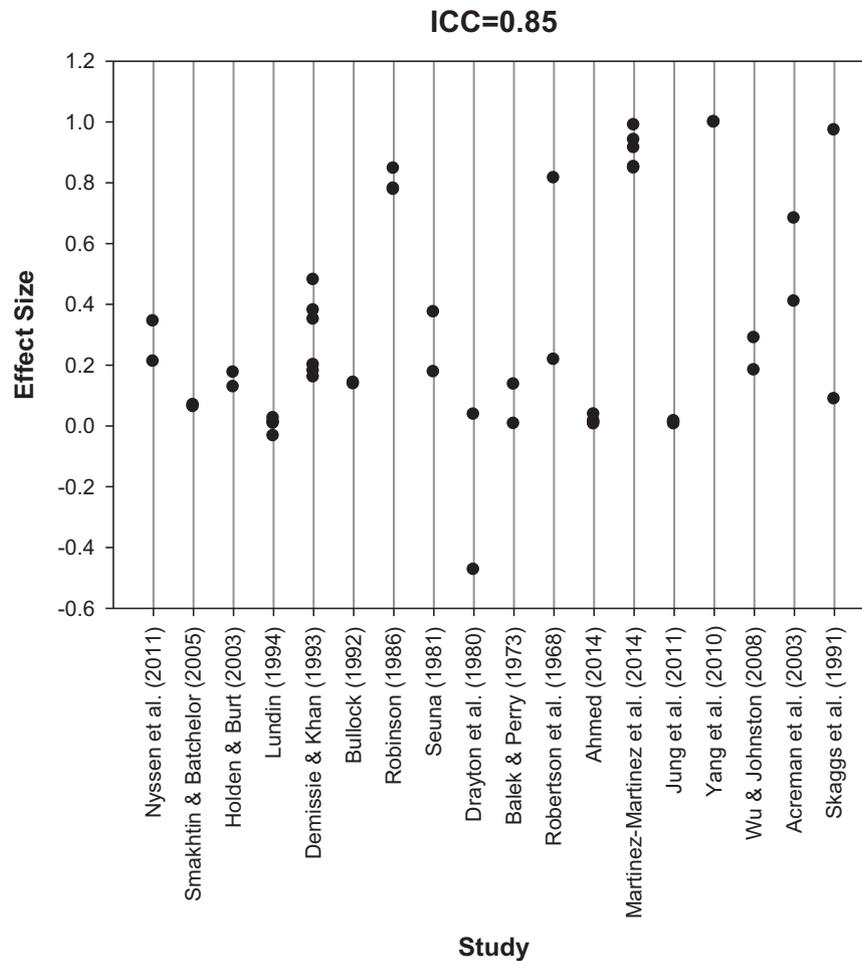
increasing spillage thresholds. For study designs that were based on a comparison between multiple treatments, eta-squared ( $\eta^2$ ) was used as the measure of effect size. This effect size measure is analogous to the coefficient of determination ( $r^2$ ) but is used for designs that compare more than two groups.

For simple CD (sCD) designs, effect sizes were calculated as the correlation between the level of one or more measurement endpoints and a single measure of wetland influence (e.g., proportion of drainage basin that is classified as wetland, number of wetlands in an area, etc.) over a set of sampling units (e.g., drainage basins, watersheds). For example, in a modelling study, Yang et al. (2010) investigated the relationship between simulated annual maximum and average daily flow and the proportion of restored wetland in the watershed. By contrast, multiple CD designs (mCD) examine the effect of more than one measure of wetland influence on flow regulation. For example, Martinez-Martinez et al. (2014) estimated the relationship between simulated streamflow reduction and both wetland area and wetland depth. For mCD designs, eta-squared ( $\eta^2$ ) was used as the effect size.

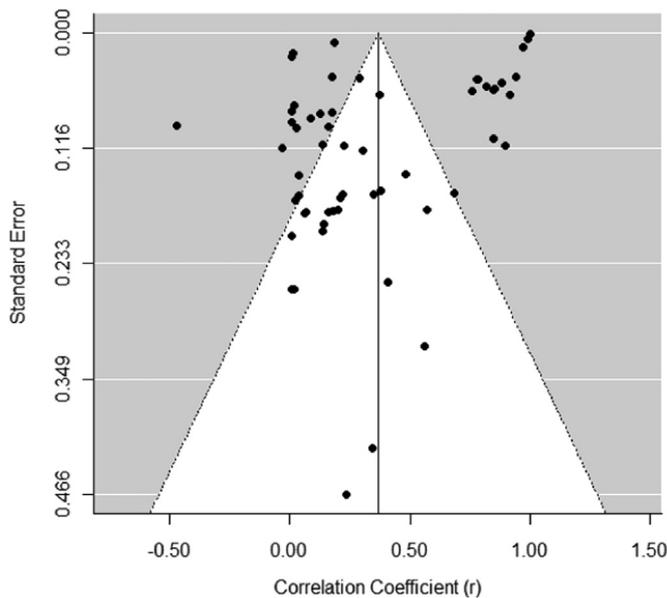
In BACI designs, one or more hydrological endpoints were compared among two or more experimental units (e.g., wetlands) before and after an intervention. For example, Robertson et al. (1968) estimated a hydrological endpoint-(time to peak) in a peat bog before and after draining and compared it to a control bog which was not drained. In BACI designs, effect sizes were calculated using the size of the treatment X site type interaction – that is, the difference between before and after means in control sites minus the difference between before and after means in impact sites (standardized mean difference).

#### Appendix E. Supplemental results tables and figures

See Figs. E1 and E2, Tables E1 and E2.



**Fig. E1.** Dot plot of estimated effect sizes for individual studies included in the analysis. Studies having multiple effect sizes (as estimated for different endpoints) show a strong intra-class correlation .



**Fig. E2.** Funnel plot of the individual correlation coefficient ( $r$ ) effect size estimates versus the corresponding standard error of the estimated effect size (reference line drawn at the random-effects model estimate  $r=0.37$ ; a pseudo confidence interval region (triangle) is drawn around this value with bounds equal to  $\pm 1.96$  SE) .

**Table E1.**

The potential for exploring associations between estimated effect sizes and candidate moderator variables for each of four datasets: weighted meta-analysis (including both empirical and modelling studies ( $k=28, N=59$ )); the subset of modelled studies ( $k=11, N=24$ ); the subset of empirical studies ( $k=17, N=35$ ); and synthetic empirical effect size dataset (includes only one effect size per study from the empirical dataset; a synthesis of the empirical dataset ( $k=N=17$ )). For a given dataset, (+) denotes a variable with within-sample variation sufficient to evaluate its association with effect size; (–) denotes a variable that could not be evaluated because the requisite information was not available for a sufficient number of studies or a variable that could not be evaluated due to insufficient within-sample variability; (n/a) denotes not applicable. For the full weighted meta-analysis, only study type was evaluated, as all other moderator showed dramatically different distributions between empirical and modelling studies.

Dataset	Basis of inference	Hydrological endpoint (indicator)	Scale	Study design	Wetland location	Study type
Full Weighted Meta-analysis	n/a	n/a	n/a	n/a	n/a	+
Modelled	–	–	–	–	–	–
Empirical	+	+	+	+	–	–
Empirical-Synthetic	+	–	+	+	–	–

**Table E2**

Calculated synthetic effect sizes (Fisher's  $z$ ) for empirical ( $k=17$ ) and modelling ( $k=11$ ) studies based on estimated intraclass correlations of 0.84 (empirical) and 0.88 (modelling). Also shown are the associated within-study variances ( $V_z$ ).

Study type	Reference	$z$	$V_z$
Empirical	Nyssen et al. (2011)	0.29	0.06
Empirical	Kværner and Kløve (2008)	0.31	0.04
Empirical	Shantzer and Price (2006)	0.65	0.33
Empirical	Smakhtin and Batchelor (2005)	0.07	0.03
Empirical	Holden and Burt (2003)	0.15	0.01
Empirical	Iritz et al. (1994)	0.63	1.00
Empirical	Lundin (1994)	0.003	0.002
Empirical	Demissie and Khan (1993)	0.31	0.006
Empirical	Bullock (1992)	0.14	0.02
Empirical	Lundin and Bergquist (1990)	0.24	1.00
Empirical	Jackson (1987)	1.00	0.03
Empirical	Robinson (1986)	1.11	0.03
Empirical	Seuna (1981)	0.29	0.01
Empirical	Drayton et al. (1980)	-0.24	0.03
Empirical	Burke (1975)	0.23	0.01
Empirical	Balek and Perry (1973)	0.07	0.04
Empirical	Robertson et al. (1968)	0.68	0.03
Modelled	Ahmed (2014)	0.02	0.007
Modelled	Martinez-Martinez et al. (2014)	1.68	0.02
Modelled	Jung et al. (2011)	0.01	0.03
Modelled	Wang et al. (2010)	0.02	0.03
Modelled	Yang et al. (2010)	3.6	0.23
Modelled	Wu and Johnston (2008)	0.24	1.00
Modelled	Yu et al. (2006)	1.39	0.06
Modelled	Acreman et al. (2003)	0.63	0.10
Modelled	Vinning (1998)	0.16	0.01
Modelled	Skaggs et al. (1991)	1.11	0.04
Modelled	Ogawa and Male (1986)	1.45	1.00

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