

Impacts of human-induced environmental change in wetlands on aquatic animals

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ABSTRACT

Many wetlands harbour highly diverse biological communities and provide extensive ecosystem services; however, these important ecological features are being altered, degraded and destroyed around the world. Despite a wealth of research on how animals respond to anthropogenic changes to natural wetlands and how they use created wetlands, we lack a broad synthesis of these data. While some altered wetlands may provide vital habitat, others could pose a considerable risk to wildlife. This risk will be heightened if such wetlands are ecological traps – preferred habitats that confer lower fitness than another available habitat. Wetlands functioning as ecological traps could decrease both local and regional population persistence, and ultimately lead to extinctions. Most studies have examined how animals respond to changes in environmental conditions by measuring responses at the community and population levels, but studying ecological traps requires information on fitness and habitat preferences. Our current lack of knowledge of individual-level responses may therefore limit our capacity to manage wetland ecosystems effectively since ecological traps require different management practices to mitigate potential consequences.

We conducted a global meta-analysis to characterise how animals respond to four key drivers of wetland alteration: agriculture, mining, restoration and urbanisation. Our overarching goal was to evaluate the ecological impacts of human alterations to wetland ecosystems, as well as identify current knowledge gaps that limit both the current understanding of these responses and effective wetland management. We extracted 1799 taxon-specific response ratios from 271 studies across 29 countries. Community- (e.g. richness) and population-level (e.g. density) measures within altered wetlands were largely comparable to those within reference wetlands. By contrast, individual fitness measures (e.g. survival) were often lower, highlighting the potential limitations of using only community- and population-level measures to assess habitat quality. Only four studies provided habitat-preference data, preventing investigation of the potential for altered wetlands to function as ecological traps. This is concerning because attempts to identify ecological traps may detect previously unidentified conservation risks. Although there was considerable variability amongst taxa, amphibians were typically the most sensitive taxon, and thus, may be a valuable bio-indicator of wetland quality. Despite suffering reduced survival and reproduction, measures such as time to and mass at metamorphosis were similar between altered and reference wetlands, suggesting that quantifying metamorphosis-related measures in isolation may not provide accurate information on habitat quality.

Our review provides the most detailed evaluation to date of the ecological impacts of human alterations to wetland ecosystems. We emphasise that the role of wetlands in human-altered ecosystems can be complex, as they may represent important habitat but also pose potential risks to animals. Reduced availability of natural wetlands is increasing the importance of altered wetlands for aquatic animals. Consequently, we need to define what represents habitat quality from the perspective of animals, and gain a greater understanding of the underlying mechanisms of habitat selection and how these factors could be manipulated. Furthermore, strategies to enhance the quality of these wetlands should be implemented to maximise their conservation potential.

Key words: ecological trap, wildlife, HIREC, habitat, human-induced rapid environmental change, habitat management, agriculture, mining, urbanisation, restoration.

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I. INTRODUCTION

Humans have altered and are continuing to alter natural environments at unprecedented rates, with significant negative impacts on animals (MEA, 2005; Pereira *et al.*, 2010). Wetlands in particular harbour highly diverse biological communities and provide extensive ecosystem services such as water purification, flood abatement and climate regulation (Costanza *et al.*, 1997; Zedler & Kercher, 2005). However, they are frequently degraded and destroyed, with over 50% of total wetland surface lost during the last century (Mitsch & Gosselink, 2007). Consequently, declines in wetland-dependent species are some of the greatest recorded, and this, along with the simultaneous loss of ecosystem services, has led to a surge in efforts to protect, create, and restore wetlands (MEA, 2005).

Ecological restoration and rehabilitation are becoming necessary to conserve and enhance biological populations and ecosystem services in an increasingly human-dominated world. Globally, significant resources are invested in wetland restoration (Groot *et al.*, 2013), with common strategies involving altering hydrological regimes (Armitage *et al.*, 2007; Raposa, 2008), restoring topography (Meyer & Whiles, 2008; Español *et al.*, 2015), planting vegetation (Spieles,

Coneybeer & Horn, 2006), and removing exotic species (Maezono & Miyashita, 2004; Curado *et al.*, 2014). Recent evidence suggests that wetland restoration can effectively promote biological enhancement and the re-establishment of ecosystem services; however, recovery may be slow, incomplete and variable among taxa (Moreno-Mateos *et al.*, 2012; Meli *et al.*, 2014).

While wetlands can be managed to promote wildlife, they can also provide a range of ecosystem services that are harnessed and exploited by humans (Hammer, 1989; Vymazal, 2009; Vymazal & Březinová, 2015; Odum, 2016). For example, wetlands are created to store and treat agricultural wastes, stormwater run-off, and fluid tailings produced during mining activities (Hammer, 1989). Although often not designed with the purpose of supporting and conserving wildlife, these wetlands often do attract animals, as they can superficially resemble natural wetlands or contain the features used by animals when selecting habitats (Bendell-Young *et al.*, 2000; Thiere *et al.*, 2009; Scheffers & Paszkowski, 2013). Consequently, these wetlands may provide important habitat, enhancing connectivity and promoting biodiversity and population persistence (e.g. Thiere *et al.*, 2009). For example, Dolny & Harabis (2012) observed more than twice as many dragonfly species in mine

subsidence pools compared to reference wetlands, likely due to environmental heterogeneity caused by a specific abiotic succession process occurring following mining. Given these kinds of findings, there has been considerable interest in combining the promotion of wildlife with pollution management (i.e. multi-objective management; Benyamine, Backstrom & Sanden, 2004).

However, since these wetlands are often (i) designed to store and/or treat pollutants, (ii) created in areas prone to contamination, and (iii) subject to human interference, animals may also be exposed to unfavourable conditions inducing both lethal and sub-lethal effects (Hopkins, Congdon & Ray, 2000; Laposata & Dunson, 2000; Dods *et al.*, 2005). For example, stormwater-treatment wetlands are common throughout many urban landscapes and receive run-off rich in contaminants such as heavy metals, pesticides and salts that can impact animal fitness (Sparling, Eisemann & Kuenzel, 2004; Snodgrass *et al.*, 2008; Gallagher *et al.*, 2014). Therefore, there is potentially a mismatch between the primary intended purpose of these wetlands and their performance as suitable habitats for animals.

The impacts on animals of low-quality wetlands will be further exacerbated if animals do not recognise them as being of poor quality and select them over more suitable habitat (i.e. an 'ecological trap'; Battin, 2004). Essentially, an ecological trap is a habitat that an animal finds equally or more attractive than other available habitat, despite it conferring comparatively lower fitness (equal-preference or severe trap, respectively; Robertson & Hutto, 2006). When selecting habitats, animals often use indirect cues that are assumed to reflect habitat quality accurately (Stamps, 2001; Stamps & Krishnan, 2005). However, following anthropogenic environmental modifications, previously reliable cues may no longer be accurate predictors of current habitat quality, resulting in an ecological trap (Schlaepfer, Runge & Sherman, 2002; Robertson & Hutto, 2006).

For example, insects such as mayflies are attracted to polarised light that guides them to aquatic breeding habitats (Schwind, 1991). However mayflies can be attracted to horizontally polarised light reflected from asphalt roads, where they consequently lay their eggs, with no chance of survival (Kriska, Horvath & Andrikovics, 1998). Ultimately, traps can lead to local extinctions, as individuals are 'drawn' into poor habitats that induce fitness costs such as reduced survival or reproduction (Battin, 2004), and these local effects can scale up to compromise metapopulation growth and persistence (Hale, Treml & Swearer, 2015b). In this regard, ecological traps can perform analogously to 'preferred sinks' in a metapopulation context (Delibes, Gaona & Ferreras, 2001).

Ecological traps form in one of three ways: cues change to increase habitat attractiveness while quality is unchanged; cues remain the same, retaining habitat attractiveness while quality reduces; or cues change to make habitats more attractive and habitat quality decreases simultaneously (Robertson & Hutto, 2006). Despite increasing evidence of the prevalence of ecological traps, there are very few

examples from aquatic systems (Hale & Swearer, 2016), potentially reflecting the relative difficulty in quantifying individual fitness and preferences in aquatic systems, the fact that ecological trap theory was initially tested using terrestrial taxa (e.g. Dwernychuk & Boag, 1972), or perhaps that traps simply do not occur frequently within aquatic systems.

Regardless of the underlying reason(s), aquatic systems in general, and wetlands in particular, are undergoing substantial environmental change and are becoming highly altered environments. As such, some authors have suggested that altered wetlands have considerable potential to function as ecological traps (Snodgrass *et al.*, 2008; Hale *et al.*, 2015a). This potential is heightened for human-altered wetlands since they often superficially resemble natural, high-quality wetlands (often intentionally through environmental manipulation), and thus likely contain cues that animals use when selecting habitats (e.g. abundant native vegetation). Even restoration may result in the formation of traps *via* the re-introduction of positive habitat selection cues to inappropriate habitats while attempting to reach some historic, pre-degraded condition (Hale & Swearer, 2017).

Although human-altered wetlands often have cues indicative of a high-quality habitat, they often contain factors – potentially undetectable – that severely impact the fitness of animals, such as pollution and exotic predators (Hale *et al.*, 2015a). Thus, the fact human-impacted wetlands may harbour abundant and diverse wildlife may not necessarily equate to long-term population persistence if individual fitness is compromised within these habitats. We currently lack a quantitative assessment of the community-, population-, and individual-level responses by animals within human-altered wetlands compared to reference wetlands. Just as judging ecosystem health using a single metric may skew perception (Palmer & Febria, 2012; O'Brien *et al.*, 2016), assessing the suitability and condition of a wetland using animal abundance or biodiversity alone may be misleading, particularly if they are functioning as ecological traps.

To address these knowledge gaps, we examine how human-induced alterations to wetlands are affecting animals at multiple levels of organisation. We conducted a global meta-analysis to address: (i) where and with which taxa current research is being undertaken to examine animal responses to wetland alteration; (ii) the characteristics of study designs [i.e. design type: before/after–control/impact (BACI) *versus* control/impact (CI) *versus* before/after (BA)] implemented to measure animal responses to wetland alteration; (iii) how key drivers of wetland alteration affect animal populations and communities; (iv) how these drivers affect the fitness of individuals that inhabit impacted wetlands; (v) whether there is significant taxonomic variability in responses, and if so, which are the most sensitive taxa; and (vi) whether animals find altered wetlands equally or more attractive than comparable reference wetlands. Our review represents an important assessment of the current state of knowledge regarding the responses of animals to

human-induced changes to wetlands, and highlights several knowledge gaps that limit current understanding of these responses. By investigating habitat preferences, we aim to evaluate how broad-scale changes to wetlands could lead to the formation of ecological traps.

II. METHODS

(1) Literature search

Wetlands are created for, and influenced by, numerous anthropogenic activities, and we were interested in collecting information on as many of these (hereafter ‘drivers’ of change) as possible. We performed a literature search on 24th January 2017 using *ISI Web of Science* and the following term: (*urban* OR agricultur* OR rural OR industr* OR city OR cities) AND (wetland* OR pond* OR pool* OR floodplain* OR swamp* OR peatland* OR marsh*) AND (mining OR development OR infrastructure OR extract* OR agricultur* OR urban* OR pollution OR herbicide* OR insecticide* OR pesticide* OR industr* OR climate* OR treatment OR stormwater OR degrade* OR impact* OR alter* OR chang* OR construct* OR creat* OR restor* OR manag* OR artificial OR replant* OR rehabilitat*) AND (animal* OR amphib* OR turtle* OR reptile* OR mammal* OR bird* OR insect* OR beetle* OR arthropod* OR *vertebrate* OR fish) AND (biodiversity OR abundance OR density OR richness OR fitness OR breed* OR reprod* OR growth OR surviv* OR mortalit* OR death* OR birth* OR spawn* OR matur* OR develop* OR metamorph* OR fecund* OR select* OR choice* OR prefer* OR settle* OR coloni* OR recruit*). Initial results were filtered to only include the research areas of environmental sciences, ecology, biodiversity conservation, marine & freshwater biology, developmental biology, agriculture, zoology, reproductive biology, physiology, water resources, forestry, behavioural sciences, and toxicology, with no restriction on publication date. In addition, we examined the reference lists of selected studies, including related reviews and meta-analyses. Because the vast majority of studies were conducted on amphibians within an agricultural context, our subsequent search of bibliographies was biased towards this taxon and driver combination. Excluding duplicates, we were left with a pool of 32,166 potentially relevant studies. The PRISMA flow diagram (Moher *et al.*, 2009) shows the procedure used for selection of studies for systematic review (Fig. 1).

(2) Data extraction and classification

To be included, we required a study to have published original quantitative data on animal (zooplankton excluded) communities, populations or individuals within human-impacted and comparable reference wetlands (see Table 1), or animal responses to wetland contaminants associated with key drivers of environmental change (field or laboratory based). In addition, the individual effects of drivers had to be discernible (i.e. non-independent,

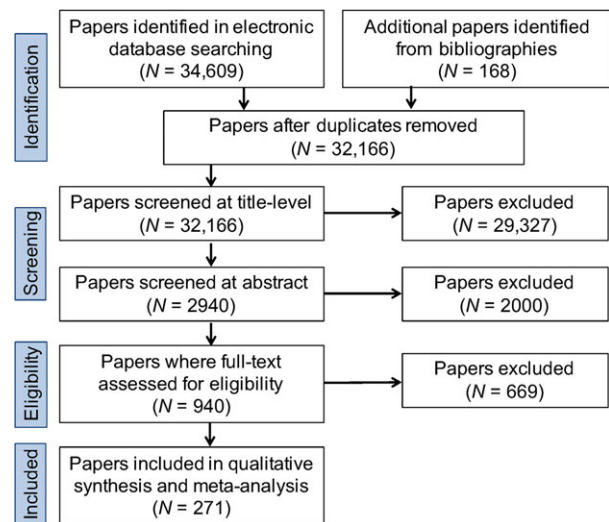


Fig. 1. PRISMA flow diagram showing the procedure used for selection of studies for systematic review and meta-analysis.

multi-driver studies were excluded). Studies comparing wetlands to lotic reference sites were excluded due to the likelihood of confounding differences between habitat types. Preliminary assessment of the database revealed that four key drivers of change would have sufficient data to conduct analyses (restoration, agriculture, mining and urbanisation), so studies relating to other drivers of change (e.g. hydrology manipulation, acidification, horse grazing) were recorded but not included in the meta-analysis. A range of information was extracted from each study where possible, including: location (continent and country), year of study, time since the alteration occurred (years), size and number of impacted and reference wetlands, taxonomic group of the animals studied, and biological response type (see online Supporting Information, Appendix S1 and Table S1). Restored wetlands may be compared to reference or degraded wetlands (see Table 1 for comparator descriptions), and separate data were extracted for both.

Most studies provided overall community or population-level metrics (e.g. richness and density) only for broad taxonomic groups (e.g. amphibians, birds, macroinvertebrates, etc.). If data on multiple species within a taxon were provided in a given study, we summed raw data to provide a single measure for each broad taxonomic group. Given the limited data on fitness measures (e.g. survival and growth), each species was treated as a separate data point. To enhance readability, herein we refer to fitness impacts as being a consequence of inhabiting wetlands affected by the drivers (i.e. amphibian survival was compromised within agricultural wetlands), despite data from manipulative laboratory experiments also contributing to the results.

(3) Effect-size calculation and statistical analysis

(a) Overall driver effects

We extracted data from impact and reference groups from the text, tables or figures (using open-source graphical

Table 1. Driver descriptions with definition of control sites used, the total number of studies data were extracted from (Total), and the number of these quantifying population-level (Popn; e.g. density), community-level (Comm; e.g. richness), fitness (Fit; e.g. survival), and habitat preference (Pref; e.g. site fidelity) measures. Years refers to time since the alteration occurred (median and range). Data are difficult to collect for agriculture and urbanisation, presumably because these are on-going, indistinct processes and therefore determining time since impact is inherently difficult. Asterisks indicate where data were scarce and so means are not provided

Driver	Description	Controls	Total	Popn	Comm	Fit	Pref	Years
Restoration	Any attempt to enhance the quality of wetlands, including both the reparation of ecosystem processes, services, and productivity, as well as restoring wetlands to some pre-existing condition. Primarily removing exotic species, marsh terracing, altering hydrology or planting vegetation. Also includes wetlands created primarily for ecological/environmental benefit, often replacing those destroyed during mitigation and translocation activities	Reference: natural wetlands typically in forested landscapes Degraded: pre-restored or unrestored sites similar to pre-restored conditions	76	54	53	5	1	Reference: 3 (<1–28) Degraded: 2.5 (<1–22)
Mining	Wetlands created for mining purposes or those impacted directly by mining. Primarily includes wetlands impacted by coal ash/combustion/strip mining and oil sands effluent	Natural wetlands in areas of natural vegetation such as meadows and forests. Control sites were not significantly impacted by anthropogenic activities, and were classified as suitable control sites by authors	32	7	9	23	0	13.75 (3–30)
Urbanisation	Wetlands created to treat stormwater/wastewater and those directly impacted by urban and/or industrial activities		50	18	22	21	1	*
Agriculture	Not applied: wetlands created for agricultural purposes or those impacted directly by agriculture. Includes natural or constructed wetlands in crop-land/farmland/ricefields influenced by pesticides, grazing, etc. Also includes raising animals in sediment/water collected from agricultural wetlands		68	28	52	11	0	*
	Applied: adding agricultural contaminants to wetlands, mesocosms or microcosms	No contaminant added	58	—	—	56	2	—

digitiser software; Huwalt, 2001) of each study, allowing us to calculate response ratios (RRs). For before/after (BA) and control/impact (CI) studies:

$$\ln [RR] = \ln [B \text{ or } I] - \ln [A \text{ or } C] \quad (1)$$

and for before/after–control/impact (BACI) studies:

$$\ln [RR] = \ln [I_A/C_A] - \ln [I_B/C_B] \quad (2)$$

where $\ln[RR]$ is the log response ratio, I is the impacted site mean, C is the control/ reference site mean, A is the after mean, and B is the before mean (Hedges, Gurevitch & Curtis, 1999). As restored wetlands may be compared to reference or degraded conditions, effect sizes were calculated independently for each comparator type.

RRs greater than zero thus indicate a positive response to the driver of wetland alteration within impacted sites compared to reference sites (CI studies), or for post-impact compared to pre-impact conditions (BA studies). A log RR cannot be defined for situations when the numerator or denominator is zero. Adding a constant to these values can lead to serious bias (Rosenberg, Rothstein & Gurevitch, 2013), so we took the more conservative approach of excluding these data (for community- and population-level measures) from further analysis. However, only 10 RRs (0.56%) were excluded from the main analyses.

For fitness measures, if there was a zero value for either the impact or reference site for a percentage measure (e.g. percentage of frogs with abnormalities), we converted the two values to represent the opposite (i.e. percentage of frogs without abnormalities), and then reversed the sign of the resultant RR. We also reversed the sign of mortality RRs so that they were directly comparable to survival RRs. For studies with multiple unpaired reference sites, we averaged data from reference sites and calculated a RR for each impacted site. Although this can create issues with non-independence, our modelling approach takes this into account (see Section II.3d).

Given the biphasic life cycle of amphibians, data were initially extracted separately for larval and adult stages. However, drivers and metrics were typically heavily biased; for example, 96.9% of agricultural fitness RRs (metamorphosis-related RRs excluded) focused on larval stages, while 74.4% of community/population-level responses did not provide separate data on larvae and adults. Preliminary analyses revealed that life-history stage was not in any of the selected models, and consequently, if studies examined responses for multiple life stages, we averaged RRs to provide one effect size for each response measure.

For studies investigating the impact of contaminants (largely agricultural pesticides and fertilisers), we first calculated separate RRs for each concentration tested, and then used the mean of these RRs for each contaminant in the formal meta-analysis. If studies included concentrations beyond those realistic in the environment as determined by the authors (typically based on levels observed within

the study region), no RR was calculated for that particular concentration. In this way, the averaged RR is indicative of that contaminant at a mid-range environmentally relevant concentration, and studies that tested numerous nominal concentrations were given no additional weighting in the analyses. Studies testing multiple contaminants independently had individual RRs calculated for each, as well as a RR calculated for each separate combination when interactions (i.e. two or more contaminants simultaneously) were investigated. If contaminant exposure was crossed with another factor of little interest here (e.g. the presence of predators; Relyea, 2005c), a RR was only calculated for the ‘simplest’ treatment (i.e. predator absent). Studies quantifying population-level metrics such as density following exposure to a contaminant were not included, as this response more closely quantifies survival than a population response to habitat quality. Studies exclusively determining LC_{50} (lethal concentration that will kill 50% of test subjects) values, or similar metrics, were also excluded. Studies investigating the effects of herbicides on non-target organisms without explicitly mentioning agriculture (e.g. silvicultural herbicides) were treated as agriculture, as the herbicides used were the same as those used in agriculture (almost exclusively glyphosate). Conversely, insecticides used for mosquito control and similar pests were not, as these pesticides were different to those used in agriculture.

Not all combinations of measures and taxa were exposed to each driver of wetland alteration precluding the exploration of complex interactions. Instead, we examined taxon-specific community-, population- and individual-level responses to each driver independently. For each taxon, we constructed a generalised linear mixed-effects model with measure (e.g. density and biomass for ‘population’) fitted as a fixed effect, and site (either wetland or treatment type) nested within study (reference) fitted as a random effect (Mengersen, Jennions & Schmid, 2013a). We produced unbiased parameter estimates and 95% confidence intervals using restricted maximum-likelihood estimation (REML) and suppressed intercepts. When sufficient data were not available to run full models, complexity was reduced (e.g. by removing the nested term) so that model estimates and variances could still be extracted (estimates from reduced models are identified within the figures). We calculated conditional r^2 -values according to Nakagawa & Schielzeth (2013), and examined funnel plots to assess publication bias (Figure S1; Stern, Egger & Davey-Smith, 2001). We performed analyses using the lmerTest package (Kuznetsova, Brockhoff & Christensen, 2015) in R v.3.2.2 (R Development Core Team, 2015) to build models and extract least-squares means and confidence intervals (Stanley & Doucouliagos, 2015).

(b) *Amphibian metamorphosis*

Amphibians were the only taxon for which data on metamorphosis were provided. We analysed measures related to metamorphosis by fitting driver (three categories: agriculture, mining and urbanisation; no data were available

from studies on restoration) and measure (four categories: mass at, length at, and time to metamorphosis, and developmental stage) as fixed effects, and a unique identifier for each site nested within study as a random effect. We fitted competing models with different fixed-effects structures and compared them using Akaike's Information Criterion corrected for small sample sizes (AIC_c; Burnham & Anderson, 2002). We rescaled these values as the difference between each model and the model with the lowest AIC_c (ΔAIC_c) for a given data set.

(c) Contaminant-applied versus not-applied studies

Due to the large number of studies on amphibians and agriculture, and to justify the inclusion of studies that applied wetlands contaminants (Applied) to the study system, we examined differences in amphibian fitness based on Applied studies to studies on amphibian fitness within agricultural wetlands to which no contaminant was added (i.e. Not-applied studies). We fitted study design (two categories: Applied and Not applied) and measure (nine categories: abnormalities, developmental stage, growth, mass at metamorphosis, reproduction, size, length at metamorphosis, survival and time to metamorphosis) as fixed effects, and a unique identifier for each site nested within study as a random effect. Similar to the amphibian metamorphosis analysis, we compared competing models using Akaike's Information Criterion.

(d) Weighting and non-independence

In general, RRs based on larger sample sizes should contribute more weight to the overall estimate than those based on smaller sample sizes, as variance is typically reduced as sample size increases. Although weighting often improves the precision of model estimates, unweighted approaches still produce unbiased mean estimates (Noble *et al.*, 2017). When variance estimates are not provided within studies, alternative weighting approaches can be used, such as one based on sample size (Mengersen, Schmidt & Jennions, 2013b). However, if incorporating weights would lead to the exclusion of too many studies that do not provide measures of sample size or variance, unweighted analyses can still be informative (e.g. Shantz, Lemoine & Burkepile, 2016).

Here, many of the studies (including fitness examinations in the field) did not report sufficient information to calculate estimates of variance, and others examined responses in impact wetlands relative to a single control wetland ($N_C = 1$). These two issues are relatively common in ecological studies on large study systems (i.e. whole wetlands; Moreno-Mateos *et al.*, 2012). This largely precluded the calculation of standard weightings used in formal meta-analyses (see Lajeunesse, 2011, 2015). Instead of omitting a high proportion of studies or conducting unweighted analyses, we calculated weights based on the sum of sample sizes (Stanley & Doucouliagos, 2015).

Given we had many cases where $N_C = 1$ (since we calculated a separate RR for each impact site), this weighting

effectively down-weighted these estimates relative to a ratio based on the average of multiple sites, helping to reduce issues with non-independence. In addition, we incorporated two unique identifiers as a random effect, where 'site' was nested within 'study'. Site nested within study accounted for any correlation amongst observations at a given site or treatment, and accounted for common local environmental or contextual effects. The study random effect accounted for any systematic differences due to common regional environmental conditions or study-specific methodologies or biases. For example, if a study reported fitness data from multiple species within a single mesocosm, these RRs would have the same site and study identity, whereas if a study reported data from multiple species raised in different mesocosms, the RRs would have different site but the same study identifier.

Our model structure therefore allowed us to analyse the multiple RRs from within a given study rather than having to aggregate data to a single mean value per study, and ultimately accounted for non-independence of multiple entries extracted from the same study, and multiple studies conducted at the same site (Krist, 2011; Davidson *et al.*, 2017). Furthermore, since our models used maximum likelihood methods, studies were automatically (implicitly) weighted by the uncertainty of the estimates, since the regression analyses, and the variation in the regression estimates, were included as part of the model (Mengersen *et al.*, 2013a).

III. RESULTS

(1) Summary information

Of the studies that met our criteria, 271 fell within one of the four main drivers (indicated with asterisks in the Reference list): agriculture (128 studies), mining (31), restoration (74) and urbanisation (50). Note that the sum of studies does not equal 271, as some studies recorded separate data for multiple independent drivers. The majority of studies were conducted in North America (70.2%), followed by Europe (13.8%), Australia (5.3%), South America (5.0%), Africa (2.8%) and Asia (2.8%; Fig. 2). CI study designs were the most frequent (95.1%), followed by BACI (3.1%) and BA (1.8%). Studies primarily reported data at the community (33.2%), population (33.5%) and individual level (32.2%), with fewer reporting data on habitat preference (1.1%), and considerable variability in taxon-specific research effort (Fig. 2). Note that of these studies, many provided data at multiple levels of organisation. Only one study provided the information required to test for an ecological trap (Severns, 2011), albeit using fitness data published in an earlier paper by the same author (Severns, Boldt & Villegas, 2006).

Conditional r^2 -values describing the proportion of variance explained by both the fixed and random factors in each taxon-specific model, along with the number of RRs, are provided in Table 2. These values provide an absolute value for the goodness-of-fit of each taxon-specific model and

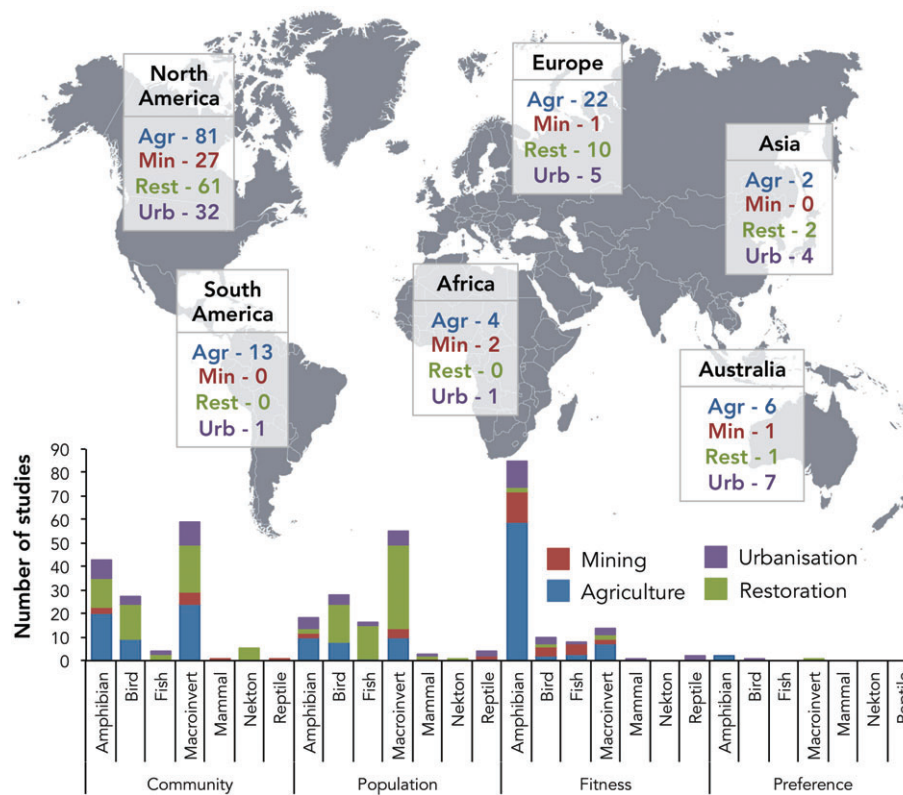


Fig. 2. Geographical distribution of studies investigating the impact of each key driver of wetland alteration on animal communities, populations, and individual fitness and preference, and the taxonomic group by response type measured. Agr, agriculture; Min, mining; Rest, Restoration; Urb, urbanisation. Several studies investigated the effects of multiple drivers independently, utilised multiple study design types, or studied multiple taxonomic groups, so totals based on the figure columns will not equal the total number of studies in the meta-analysis. Note that the number of studies investigating agricultural impacts on amphibian fitness is artificially inflated by the intentionally biased searching for studies outlined in Section II.1.

describe the proportion of variance explained by both the fixed and random factors (Nakagawa & Schielzeth, 2013). Model structure and a full summary output is provided in Appendix S2, and the extracted data are included in Appendix S1.

(2) Communities

Grand means (i.e. all taxa combined) for the three community-level measures (Shannon diversity, richness and evenness) were largely comparable between impacted and reference wetlands (Fig. 3A). Exceptions to this include reduced community richness within agricultural wetlands, increased richness in restored relative to degraded wetlands, and greater community evenness within agricultural wetlands. Amphibians exhibited similar trends, whereby the richness and evenness of communities was lower and higher, respectively, within agricultural wetlands, while no other driver affected amphibian communities significantly (Fig. 3B). Bird communities too were similar between impacted and reference wetlands, with lower richness and diversity within agricultural wetlands and higher richness in restored relative to degraded wetlands the only significant responses observed (Fig. 3C).

Comparatively, relatively few data were available for fish communities, although there was evidence for reduced Shannon diversity within urban wetlands, and increased richness within restored wetlands (Fig. 3D). Macroinvertebrate communities were less rich and less even in urban wetlands while restored wetlands had greater evenness relative to reference conditions (Fig. 3E).

(3) Populations

Similar to community-level responses, grand means for population-level measures were similar between impacted and reference wetlands (Fig. 4A). Compared to degraded wetlands, animal population density and biomass was significantly higher in restored wetlands (Fig. 4A). There was, however, greater evidence for variability amongst taxa for population densities in particular. Compared to reference wetlands, amphibian densities were higher within restored wetlands, and similar within urban, mining and agricultural wetlands (Fig. 4B). Birds showed similar trends, whereby densities within restored wetlands were higher than in degraded wetlands (but not reference wetlands), while those within urban and agricultural wetlands were comparable to reference sites (Fig. 4C).

Table 2. Conditional r^2 -values describing the proportion of variance explained by both the fixed (measure: richness, survival, growth, etc.) and random factors (reference) for each model used to estimate means and confidence intervals for response ratios (RRs) in Figs 3–5 (i.e. amphibian metamorphosis RRs not included). Some r^2 -values could not be calculated due to some variance components equalling zero. Values in parentheses are the number of RRs within each model. Note that the total number of RRs for each grand mean does not always equal the sum of taxa RRs as some taxa (e.g. nekton, mammals and reptiles) contributed to grand means, but could not be analysed individually due to insufficient replication

Driver	Metric	Taxa				
		Amphibian	Bird	Fish	Macroinvert	Grand mean
Agriculture	Community	0.88 (125)	0.72 (17)	—	0.17 (41)	0.71 (184)
	Population	0.98 (11)	0.92 (10)	(1)	0.789 (14)	0.96 (37)
	Fitness	0.59 (421)	(5)	(3)	0.43 (36)	0.64 (465)
Mining	Community	0.97 (7)	—	—	0.79 (32)	0.79 (44)
	Population	(2)	—	—	0.78 (23)	0.87 (28)
	Fitness	(40)	0.84 (45)	(45)	(2)	(132)
Restoration reference	Community	0.59 (26)	(26)	(11)	(83)	0.43 (160)
	Population	(2)	(31)	(38)	0.58 (102)	(184)
	Fitness	(19)	(2)	—	(9)	(30)
Restoration degraded	Community	(3)	0.73 (7)	0.01 (15)	0.40 (14)	0.52 (47)
	Population	—	(17)	(31)	0.53 (32)	0.59 (90)
Urban	Community	0.89 (12)	(3)	0.71 (8)	(26)	0.54 (50)
	Population	(4)	0.93 (13)	0.96 (8)	(10)	0.87 (39)
	Fitness	(32)	(11)	(3)	(30)	(80)
$N_{\text{total}}(\text{RR})$		704	187	163	454	1573

The density and biomass of fish populations were lower within urban wetlands, while densities were higher in restored wetlands compared to degraded wetlands, and also higher in agricultural wetlands (Fig. 4D). Macroinvertebrates had higher densities and greater biomasses within urban wetlands, and restored wetlands when compared to degraded comparators (but not reference comparators; Fig. 4E).

(4) Individuals

(a) Overall driver effects

Grand means revealed that overall animal fitness within altered wetlands was often significantly reduced relative to reference conditions, with the greatest impacts on survival, reproduction and an increased incidence of abnormalities (Fig. 5A). Amphibians exhibited reduced survival and more abnormalities within urban, mining and agricultural wetlands, while reproduction was lower in mining and agricultural wetlands (Fig. 5B). Although based on limited data (and thus limited statistical power), the fitness of amphibians within restored wetlands was comparable to reference sites.

Overall, the fitness of birds was relatively comparable between altered and reference wetlands, with reproduction impacted within both mining and urban wetlands (Fig. 5C). Fish reproduction was lower in wetlands impacted by agriculture and mining, and mining also caused an increase in the incidence of abnormalities (Fig. 5D). Macroinvertebrate reproduction and survival were lower within restored and agricultural wetlands, respectively, while growth was faster in urban wetlands but slower in wetlands impacted by mining (Fig. 5E).

(b) Amphibian metamorphosis

In general, measures relating to amphibian metamorphosis (i.e. developmental stage, and mass at, length at and time to metamorphosis) were largely unaffected by drivers of wetland alteration (Fig. 6). Despite the model including measure as a factor being most supported (Table 3), no clear differences among measures were evident, and no driver consistently affected measures in the same direction (Fig. 6).

(c) Contaminant-applied versus not-applied studies

The effect of agriculture on amphibians was largely consistent between manipulative experiments looking at the fitness impacts of agricultural fertilisers and pesticides (field or laboratory based; Applied) and studies looking at the fitness impacts of agricultural wetlands without experimentally manipulating the conditions (Not applied). Although the model including the interaction between study type (Applied *versus* Not applied) and fitness measure was most supported (Table 3; Figure S2), the confidence intervals for all but one fitness measure overlapped.

(5) Habitat preference

Only four studies quantified suitable proxies for habitat preference (based on the criteria provided in Robertson & Hutto, 2006) that met our criteria for inclusion in the study [Frederick & McGehee (1994) – first site foraged (birds); Vonesh & Buck (2007) – oviposition site selection (amphibians); Severns (2011) – oviposition site selection (macroinvertebrates); Wagner & Loetters (2013) – choice experiments (amphibians)]. Consequently, not enough

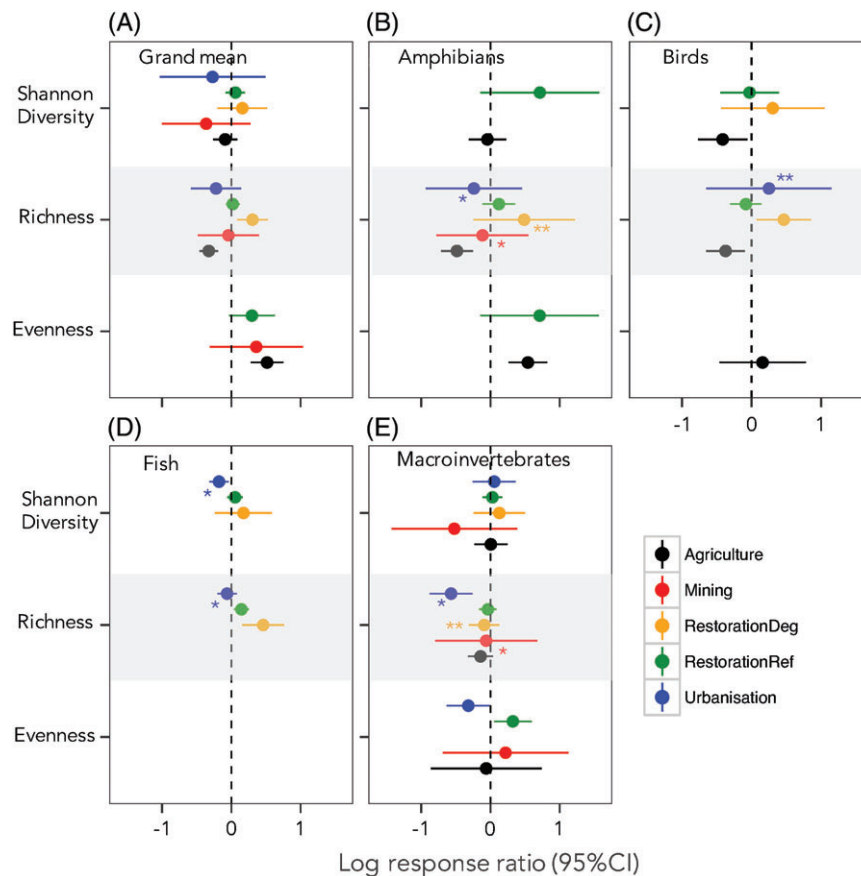


Fig. 3. Forest plots of weighted taxa-specific community-level response ratios (and 95% CI on log scale) for (A) grand means (all taxa combined), (B) amphibians, (C) birds, (D) fish, and (E) macroinvertebrates. Restored wetlands are compared to natural reference wetlands (RestorationRef), or to pre-restored or unrestored sites similar to pre-restored conditions (degraded; RestorationDeg). We used weighted linear mixed-effects models with a unique identifier for each site and study fitted as a nested random effect (site within study), and intercepts were suppressed so that we could estimate separate coefficients. Taxon-specific models with response measure as a fixed effect were fitted to produce unbiased parameter estimates and 95% confidence intervals. Grand means were estimated by removing taxa as a factor from measure-specific models. Note that when data are plotted for only one taxon, often the grand mean will differ for that response measure, as additional data from different taxa were available but without appropriate replication to analyse that taxon independently. A single asterisk identifies when the specific model used to calculate response ratio (RR) estimates had only a single random term (i.e. not nested) due to insufficient replication. A double asterisk identifies when the model had no random term fitted due to insufficient replication. A triple asterisk identifies when the estimate provided is simply the mean RR, as insufficient data were available to create a model.

habitat preference data were available to conduct formal analyses. However, on average, relative to reference sites, birds preferred foraging first in urban wastewater wetlands ($RR = 0.24 \pm 0.35$; mean \pm S.E.), butterflies preferred ovipositing within a restored marsh ($RR = 1.48$), frogs and newts avoided herbicides ($RR = -0.17 \pm 0.11$), and frogs avoided ovipositing in water contaminated with insecticides ($RR = -1.30 \pm 0.37$).

IV. DISCUSSION

(1) Summary information

Our global meta-analysis of 271 studies from 29 countries provides a comprehensive assessment of how animals

are utilising wetlands created or altered by common drivers of human-induced environmental change. CI study designs were most commonly utilised, despite the advantages of characterising background spatial and temporal variability against which researchers can assess if significant changes have occurred (i.e. a BACI design; Stewart-Oaten, Murdoch & Parker, 1986). Particularly for assessing the outcomes of ecological restoration, knowledge of pre-restoration conditions is required to account for inherent differences between control and restored sites. Without prior information, efforts to assess responses to restoration may be severely confounded despite attempts to match control and treatment sites. The apparent popularity of CI study designs may stem from a lack of foresight, with managers often not engaging ecologists early in the restoration process, removing the capacity to survey pre-restoration conditions.

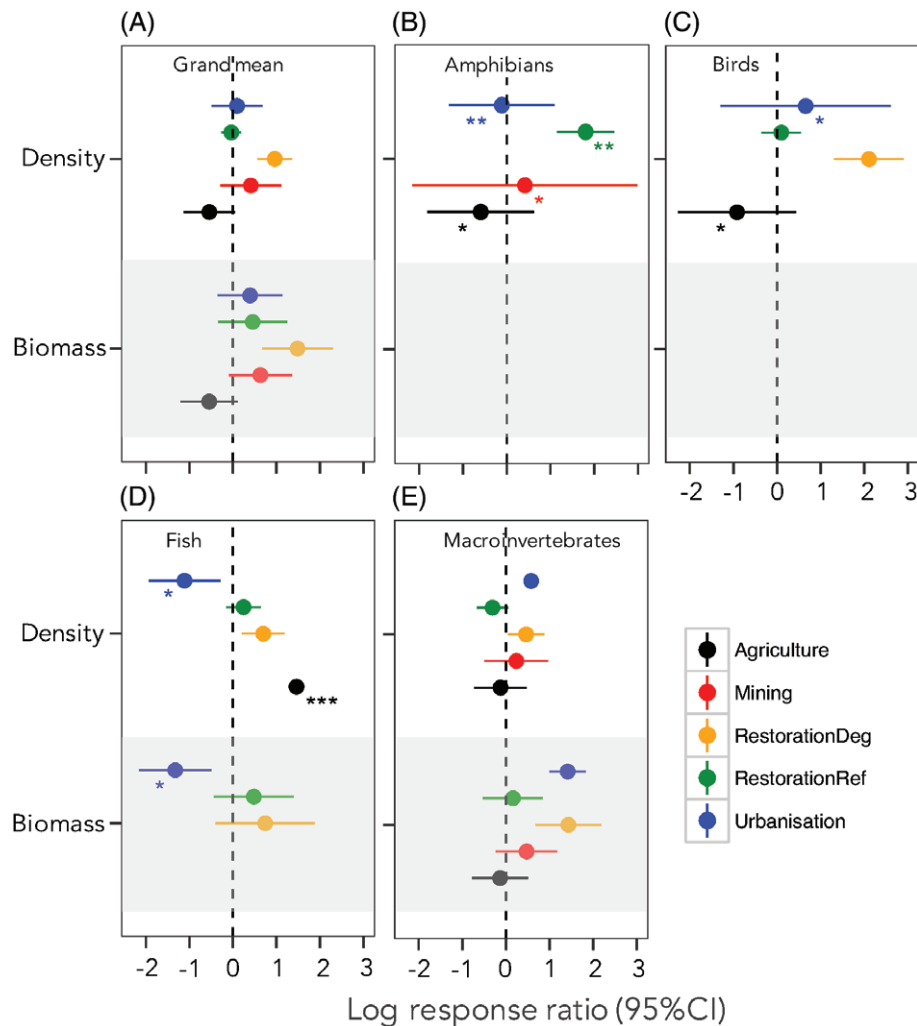


Fig. 4. Forest plots of weighted taxa-specific population-level response ratios (and 95% CI on log scale) for (A) grand means (all taxa combined), (B) amphibians, (C) birds, (D) fish, and (E) macroinvertebrates. For modelling approach and response ratio estimation, see Fig. 3 legend.

Alternatively, the costs of monitoring may far exceed the cost of restoration works, or the benefits of monitoring through time may not be as obvious. Regardless of the cause, this issue is common to restoration ecology more generally, and has been discussed elsewhere (e.g. Miller, Budy & Schmidt, 2010).

As with many ecological meta-analyses, studies were heavily biased towards North America (Lawler *et al.*, 2006; Felton *et al.*, 2009; Conrad, Christie & Fazey, 2011). It is important, however, to focus ecological monitoring in areas most susceptible to environmental degradation. For example, the majority of research monitoring the impacts of urbanisation on wetland animals was conducted in affluent, developed countries, despite current rates of urbanisation being highest in developing regions (Cohen, 2006; Parriss, 2016). The observed geographical bias towards affluent countries is not particularly surprising but does raise issues around the transferability of findings. For example, it is possible that the fitness-reducing contaminants within urban

wetlands will be more prevalent in developing countries due to comparatively lower investment in, and less advanced technology for, pollution management (Kivaisi, 2001). Increasing research effort within less-well-studied regions, and comparing findings to current research will help address this issue, and may provide justification for using data from other regions to manage wetlands elsewhere.

(2) Communities

Grand means revealed that overall Shannon diversity and richness were largely comparable between altered and reference wetlands, with richness only higher within agricultural wetlands and greater within restored relative to degraded conditions. On the other hand, evenness was greater within agricultural wetlands, as well as in restored relative to reference sites. However, comparing grand means across drivers may be problematic, as data were not available from each taxon for each driver by measure combination,

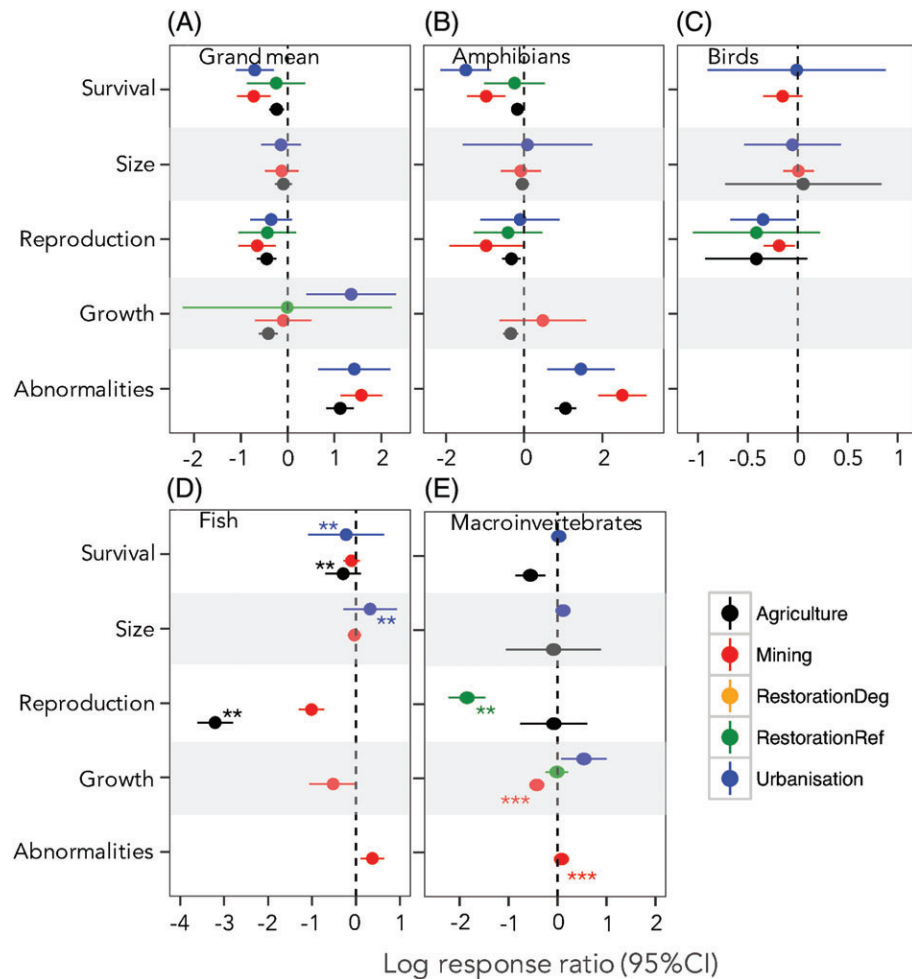


Fig. 5. Forest plots of weighted taxa-specific individual/fitness response ratios (and 95% CI on log scale) for (A) grand means (all taxa combined), (B) amphibians, (C) birds, (D) fish, and (E) macroinvertebrates. For modelling approach and response ratio estimation see Fig. 3 legend. Note the different x -axes to aid visualisation of each individual taxonomic response.

and because looking at such broad-scale patterns may mask potentially more relevant patterns present at finer scales.

There was little evidence for any substantial taxonomic variability in community-level responses to the four key drivers of wetland alteration. Most notably, amphibian and bird communities were less rich within wetlands affected by agriculture, and there was evidence for greater evenness of amphibian communities within these wetlands – likely the result of rarer and more susceptible species being excluded from agricultural areas, while common, hardier species remain present in relatively high and even numbers. Reductions in amphibian community richness were largely consistent for wetlands within cropland (e.g. Peltzer *et al.*, 2006; Russell & Downs, 2012) and ricefields (e.g. Moreira & Maltchik, 2014; Cunha *et al.*, 2015), and wetlands influenced by cattle grazing (e.g. Schmutzer *et al.*, 2008). Species-specific traits such as dispersal capacity, reproductive modes and individual habitat preferences will likely regulate amphibian community composition within agricultural wetlands (Burton *et al.*, 2009; Moreira & Maltchik, 2014, 2015). Koumaris

& Fahrig (2016) observed highly variable responses of amphibian communities dependent on agricultural intensity and consequently advise against generalising impacts. Therefore, despite the observed overall reduction in richness of amphibian communities, some species may be highly successful in agricultural areas and successfully persist as metapopulations (Knutson *et al.*, 2004).

Similarly, despite evidence for reduced richness and diversity of bird communities within agricultural sites, the loss of natural wetlands within these areas has meant that the conservation of wetlands within agricultural landscapes is crucial for many wild bird populations (Heimlich *et al.*, 1998; Scherr & McNeely, 2008). Like amphibians, macroinvertebrate communities were less rich and even in urban wetlands, again likely a consequence of the presence of only a few hardier species, similar to the macroinvertebrate communities found in polluted urban streams and rivers (Walsh *et al.*, 2005; Beyene *et al.*, 2009). Despite the above evidence that wetlands altered by humans can harbour communities less diverse and rich

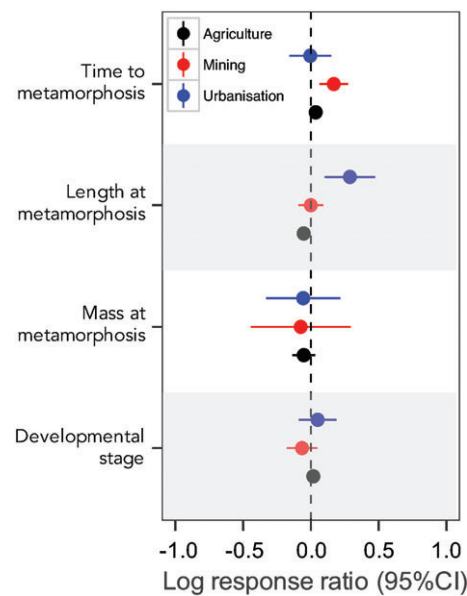


Fig. 6. Forest plots of weighted amphibian metamorphosis-related response ratios (and 95% CI on log scale) for wetlands impacted by agriculture, mining, and urbanisation. The model including the factor for measure (developmental stage, and mass at, length at and time to metamorphosis) was most supported (see Table 3). For modelling approaches and response ratio estimation see Fig. 3 legend.

than reference wetlands, many were highly comparable to their reference counterpart, and endangered species have been reported within human-altered wetlands, highlighting both their biological value and conservation potential under certain conditions (Chovanec, 1994; Chester & Robson, 2013).

(3) Populations

Overall animal population density and biomass were similar between altered and reference wetlands for all drivers

(the exceptions being a greater biomass and density in restored wetlands compared to degraded wetlands), but there was considerable taxonomic variability in responses. Generally, responses to wetland restoration were similar to those presented by Moreno-Mateos *et al.* (2012) and Meli *et al.* (2014), whereby populations within restored wetlands reached parity with those within reference wetlands, and typically surpassed those within degraded wetlands. The factors influencing wetland restoration success in terms of both biodiversity and ecosystems services have been comprehensively discussed elsewhere (see Moreno-Mateos *et al.*, 2012, 2015; Meli *et al.*, 2014).

Amphibian populations were largely unaffected by drivers of wetland alteration, although restoration activities resulted in greater population densities than those at reference sites. Wetland mitigation practices (Balcombe *et al.*, 2005b) and the restoration of peat bogs (Mazerolle *et al.*, 2006) both enhanced amphibian populations to levels surpassing reference sites. Bird populations were largely comparable between altered and reference wetlands, with restoration enhancing populations above degraded conditions and similar to reference conditions. Restoration activities here typically involved restoring tidal flow, likely leading to an increase in food supply for aquatic and semi-aquatic birds, as well as leading to a decrease in invasive vegetation (Rochlin *et al.*, 2012).

Although the density of fish was lower in stormwater and sewage effluent wetlands (i.e. urbanisation), these data are based on populations of the invasive mosquitofish, *Gambusia holbrooki*, and so in this circumstance, a lower population density may not be an ecologically negative outcome (Midgley, Burgin & Renshaw, 2014). Fish densities within agricultural wetlands were substantially higher than within respective reference wetlands, however, these data are from a single study where nutrient enrichment enhanced macroinvertebrate food supplies, and subsequently enhanced small fish populations (Rader & Richardson, 1994). Eutrophication-driven increases in primary productivity that

Table 3. Model selection based on Akaike weights adjusted for small sample sizes for: the effect of agriculture, mining and urbanisation on developmental stage, and time to, length at, and mass at amphibian metamorphosis; and the response of amphibians to agriculture when contaminants were applied or not applied to the study system. Boldface indicates the most supported model. For detailed descriptions, see Section II.3b.

Model		<i>K</i>	AICc	ΔAICc	LL
Amphibian metamorphosis					
M0	Null	4	−160.13	7.67	84.17
M1	Driver	6	−157.29	10.52	84.86
M2	Measure	7	−167.81	0	91.19
M3	Driver × measure	15	−164.62	3.19	98.59
Applied <i>versus</i> not applied					
M0	Null	4	728.63	53.43	−360.28
M1	Study type	5	727.18	51.98	−358.54
M2	Measure	12	698.74	23.54	−337.10
M3	Study type × measure	20	675.19	0	−316.87

AICc, Akaike's information criterion corrected for small sample sizes; ΔAICc, difference in AIC between model and most supported model; *K*, number of estimated parameters; LL, log likelihood of model.

benefit higher-order taxa may also be responsible for many of the trends observed here, where populations within altered wetlands are at parity with those from relatively uncontaminated reference sites.

Macroinvertebrate populations responded positively to urbanisation, largely driven by responses by numerous aquatic worm species found at high densities within wetlands impacted by a chloralkali production facility (Horne, Finley & Sprenger, 1999), and an overall greater density of macroinvertebrates within stormwater and wastewater wetlands (e.g. Kashian & Burton, 2000; Le Viol *et al.*, 2009). Like other taxonomic groups, restoration led to higher densities of macroinvertebrates compared to degraded conditions, and similar densities compared to reference conditions. Sufficient data from lower-order macroinvertebrate classifications within wetlands were unavailable to examine properly whether this was due only to increases in hardier taxa or whether entire communities benefit. Extrapolating evidence from lotic systems suggests that enhanced population densities are likely a result of increases in hardier taxa (Walsh *et al.*, 2005; Beyene *et al.*, 2009). In general, while there was significant variability amongst taxonomic groups, restored wetlands and those created for, and impacted by, agriculture, mining and urbanisation harboured relatively abundant animal populations.

(4) Individuals

Despite evidence that animal communities and populations are relatively similar in altered and reference wetlands, individual fitness measures were often lower in altered wetlands. Excluding restoration, the three other drivers of alteration – agriculture, mining and urbanisation – resulted in taxon-specific fitness reductions in at least two fitness measures. Evaluation of the fitness consequences of animals inhabiting restored wetlands was almost non-existent; only five of the 73 restoration studies we extracted data from quantified individual fitness (Petranka, Murray & Kennedy, 2003; Severns *et al.*, 2006; Desrochers, Keagy & Cristol, 2008; Rozas & Minello, 2009; Burhans *et al.*, 2010), which limited statistical analysis and the potential to make any ecologically relevant inferences.

Amphibian fitness – based primarily on larval responses – was greatly impacted within altered wetlands and by contaminants associated with common drivers of change. Amphibians are often considered particularly sensitive to environmental contamination (Blaustein, Wake & Sousa, 1994; Wake & Vredenburg, 2008; but see Kerby *et al.*, 2010), and are experiencing dramatic population declines across the globe, with approximately 40% of species facing the threat of extinction (Whitfield *et al.*, 2007; Butchart *et al.*, 2010; Monastersky, 2014). Agriculture was associated with reduced survival, reproduction and growth, while also increasing the incidence of abnormalities. Common agricultural contaminants entering water bodies can significantly impact amphibian fitness, including fertilisers (e.g. Sullivan & Spence, 2003; Griffis-Kyle & Ritchie, 2007), fungicides (Ernst *et al.*, 1991; Fioramonti *et al.*, 1997), herbicides (Mann, Bidwell & Tyler, 2003;

Brodeur *et al.*, 2009) and insecticides (Fordham *et al.*, 2001; Metts, Hopkins & Nestor, 2005).

Importantly, many of the studies contributing data to these findings involved the experimental application of agricultural contaminants (i.e. Applied studies), and thus, may have inflated estimates of amphibian fitness reductions within agricultural wetlands. However, by excluding contaminant concentrations deemed environmentally unrealistic by the authors of each study, and averaging responses to the remaining tested concentrations, fitness impacts based on these manipulative experiments were similar to those investigating the impacts of agricultural wetlands when conditions were not experimentally manipulated (i.e. Not-Applied studies). Therefore, at least for amphibians, quick and relatively inexpensive laboratory experiments testing contaminants at environmentally relevant concentrations appear to be a valuable tool to predict the fitness impacts of inhabiting wetlands affected by agriculture.

Mining also severely reduced amphibian fitness; survival and reproduction were lower and the incidence of abnormalities higher within mining wetlands than in reference wetlands. While the majority of the data were from oil sands mining, wetlands containing coal combustion waste that was high in metals and metalloids (e.g. Metts *et al.*, 2013) and mesocosms spiked with mining-derived heavy metals (Snodgrass *et al.*, 2005) also significantly reduced amphibian fitness. Oil sands process material (OSPM) contains high levels of polycyclic aromatic hydrocarbons (PAHs), various salts and naphthenic acids (NAs), all of which have been demonstrated to impact individual fitness drastically (Pollet & Bendell-Young, 2000; Siwik *et al.*, 2000; Incardona, Collier & Scholz, 2004).

As with agriculture and mining, amphibians were the taxon most susceptible to wetland alteration as a result of urbanisation, with significant reductions in survival and an increase in the prevalence of abnormalities. Amphibians are considered particularly sensitive to urbanisation because they often have low vagility, a low probability of successfully crossing roads, narrow habitat niches, and a high vulnerability to pathogens, pollutants and climate change (Cushman, 2006). Given that most of the fitness data summarised here are based on tadpoles, this vulnerability is most likely responsible for the fitness reductions observed here. Urban wetlands receive considerable run-off, either inadvertently due to high levels of impervious surfaces surrounding urban wetlands or due to urban wetlands being intentionally used to intercept pollutants before they reach stormwater and lotic systems (Fletcher *et al.*, 2015). Run-off often contains a cocktail of toxic contaminants including heavy metals, salts, hydrocarbons, fertilisers and pesticides; all of which negatively affect aquatic animals (Bishop *et al.*, 2000a,b; Lieb & Carline, 2000). Urban wetlands are also notoriously prone to exotic species introductions, where they are often invaded by non-native plants and animals *via* intentional planting or releasing pets or unintentionally *via* dispersal from upstream urban watersheds (Ehrenfeld, 2008).

Many exotic species, such as mosquitofish, are voracious predators that consume amphibian eggs, and have been implicated in dramatic population declines of native animal species (Pyke, 2008).

In general, environmental contamination is known to increase the rate of amphibian abnormalities such as malformed limbs, missing eyes, oedema, scoliosis and calcinosis (Ruiz *et al.*, 2010), and we commonly found substantially higher rates of abnormalities within altered wetlands (on average five times higher). However, these RRs may be artificially inflated. Unlike the other fitness measures analysed, it is likely that the prevalence of abnormalities would only be published when abnormalities are actually discovered (i.e. data may not be provided if no abnormalities are observed, when subsequent RRs would equal zero). Despite this, physical abnormalities can reduce survival rates and the probability of successful reproduction, and quantifying abnormalities remains a relatively simple and non-invasive method to quantify fitness (Johnson *et al.*, 2001). Therefore, although the absolute differences quantified here may be inflated, the incidence of abnormalities is undoubtedly higher within altered wetlands compared to reference wetlands, and monitoring amphibians for physical abnormalities remains a quick, non-lethal method to assess habitat quality.

One of the main reasons that monitoring programs fail is that the selection of ecological indicators to monitor responses is not well justified (Lindenmayer & Likens, 2010). Based on their higher responsiveness in comparison with other taxa, our results indicate that amphibians are sensitive indicators of environmental change. Since many studies report significant intraspecific and life-history-specific responses to wetland contaminants, using amphibians as an indicator species will require careful consideration of the species and life-history stages examined, as well as the specific fitness proxies measured. For example, exposing embryos and tadpoles to stormwater wetland sediments resulted in 100% mortality of wood frog, *Rana sylvatica*, but only sub-lethal effects in the more tolerant American toad, *Bufo americanus* (Snodgrass *et al.*, 2008). Additionally, survival of gray tree frog, *Hyla versicolor*, embryos was reduced to only 50% when exposed to stormwater pond sediments but no such decrease was observed in tadpoles (Brand & Snodgrass, 2010).

Animals in polluted environments may grow more slowly due to the expenditure of energy on detoxification (Gentes *et al.*, 2006), and we found some evidence for reduced growth of amphibians inhabiting agricultural wetlands. However, size and growth responses were largely comparable between altered and reference wetlands. Similarly, while measures associated with metamorphosis (i.e. time to, mass at and length at metamorphosis) have been shown to vary with temperature, the presence of food, the density of individuals, and hydroperiod (Edge *et al.*, 2016), we observed few difference in these measures between altered and reference wetlands despite substantial data (203 RRs). Therefore, growth or metamorphosis-related fitness proxies in isolation may not accurately reflect the overall quality

of habitats, where a diversity of factors may interact to influence developmental and growth rates (Egea-Serrano *et al.*, 2012). Conversely, fitness measures related to survival and reproduction were consistently reduced within altered wetlands, and so focusing monitoring efforts on these will provide more accurate information on the quality and suitability of individual wetlands.

Birds were less susceptible to wetland alteration than amphibians; mining and urbanisation did not influence the survival or size of individuals. This finding may reflect a lower proportion of time spent at wetlands and a greater overall capacity to move amongst habitats by birds compared to more aquatic taxa such as amphibians and fish. There was evidence for reduced bird reproduction with mining and urbanisation. OSPM-affected wetlands were again the main contributor to reductions in fitness; tree swallow, *Tachycineta bicolor*, nestlings at these wetlands suffered greater mortality; those surviving were smaller and exhibited higher hepatic detoxification activity compared to nestlings from reference wetlands (Gentes *et al.*, 2006). However, the impact of OSPM-reclaimed wetlands on tree swallow reproduction was equivocal, with another study reporting similar reproductive success at OSPM wetlands and reference wetlands, with reproduction RRs ranging from -0.09 to 0.13 ($N = 8$; Smits *et al.*, 2000).

Similar to birds, fish survival and size were comparable between altered and reference wetlands, while reproduction was significantly impacted by both agriculture and mining. The substantial decrease in fish reproduction associated with agriculture comes from a single study on bluegill (*Lepomis macrochirus*) fecundity within experimental ponds treated with atrazine (Kettle *et al.*, 1987), and results should thus be interpreted with caution. Evidence for mining impacts on fish fitness came exclusively from OSPM wetlands; fathead minnows, *Pimephales promelas*, suffered compromised reproduction (Kavanagh *et al.*, 2011), while survival, size and growth were relatively unaffected (Siwik *et al.*, 2000; Kavanagh *et al.*, 2011; He *et al.*, 2012). Additionally, the incidence of abnormalities was higher within mining wetlands for both yellow perch, *Perca flavescens* (Van den Heuvel *et al.*, 2012), and fathead minnows (Kavanagh *et al.*, 2011). The same toxic compounds prevalent within OSPM wetlands that impacted amphibian fitness may be responsible for these fitness reductions observed in fish.

Despite a wealth of macroinvertebrate community- and population-level data, individual fitness data on this taxon were relatively scarce. Butterfly egg survival was severely reduced within a restored marsh (Severns *et al.*, 2006; Severns, 2011), while the growth of shrimp and crabs was similar in restored and reference wetlands (Rozas & Minello, 2009). Significant butterfly egg mortality was attributed to restoration activities culminating in an ecological trap for this wetland-dependent species (see Section IV.5).

As seen in many other taxa, agriculture and the associated contaminants reduced macroinvertebrate survival; field and laboratory applications of fungicides (e.g. Ernst *et al.*, 1991), herbicides (e.g. Plumley *et al.*, 1980) and

insecticides (e.g. Wayland & Boag, 1990) all reduced survival rates. For example, diverse aquatic communities subjected to insecticides or herbicides during simulated oversprays resulted in the death of a large portion of the macroinvertebrate community (Relyea, 2005a). Although macroinvertebrate growth was greater within urban wetlands, estimates were exclusively from experiments on the notoriously resilient family Chironomidae (Liber *et al.*, 1996). Conversely, chironomid growth was reduced within OSPM mining wetlands (Wiseman *et al.*, 2013), indicating that urban pollutants may be less toxic than OSPM to this taxon.

Despite substantial driver-, taxon- and measure-specific variability in individual-level responses to key drivers of wetland alteration, key fitness measures within human-impacted wetlands were generally reduced, particularly for amphibians. The increasing importance of these wetlands resulting from the loss of natural wetland demands further research into their fitness impacts to determine more accurately their suitability for wildlife.

(5) Habitat preference and ecological traps

Due to accelerating habitat alteration and the increasing recognition and appreciation of ecological traps and their impacts, identifying habitat preferences has become an important component of the conservation and management of wild animal populations (Sinsch, 2014). To provide evidence that animals exhibit a preference for particular habitats, researchers can monitor settlement patterns or the distribution of dominant individuals, quantify site fidelity or temporal variance in population size, or conduct manipulative choice experiments [see Robertson & Hutto (2006) for detailed descriptions of these methods]. We identified a number of studies that discussed habitat preference based solely on abundance in particular habitats or the proportion of available habitat relative to the proportion utilised as proxies for preference. Amongst other scenarios, these methods do not account for the possibility that dominant individuals may exclude the majority of a population from the preferred habitat, or that observed patterns are in fact driven by differential post-settlement mortality (Crowe & Underwood, 1998). Therefore, these proxies are not suitable to quantify habitat preference and consequently very few studies identified here provided suitable proxies.

Only one study contained the necessary information to test ecological trap theory (i.e. fitness and habitat preference; Sievers, 2011). In this instance, preference was greater for a restored wetland within which fitness was comparatively low, resulting in the formation of an ecological trap (fitness data from this site were presented in an earlier paper by the same author; Sievers *et al.*, 2006). In this ecological trap, a butterfly preferentially oviposited on their host plant species within a restored, seasonally flooded wetland over a natural, non-flooded wetland. Egg survival in the restored habitat was seven times lower than in the natural habitat due to the impacts of seasonal flooding. In addition, within the

restored habitat, the host plant was more visible due to a lack of tall exotic grasses that were present in the natural habitat. Therefore, the cause of this ecological trap was twofold; firstly, the addition of host plants during restoration of a seasonally flooded wetland that was inappropriate for butterfly reproduction, and secondly, the devaluing of optimal breeding habitat by an exotic grass.

Maladaptive habitat selection leading to the formation of ecological traps is most likely when animals encounter cues closely resembling those that have previously been accurate indicators of favourable environmental conditions (Sih, Ferrari & Harris, 2011; Sih, 2013). In addition, the consequences of these decisions are likely to be most severe when animals select habitats with novel environmental conditions unlike those under which selection has previously acted (Ghalambor *et al.*, 2007). Therefore, any anthropogenic modification to the environment – including those with a positive environmental goal such as restoration – has the capacity to create traps.

Despite good intentions, ecological restoration may impact animal fitness because human perception of past or ideal conditions may be skewed and differ substantially from the functional habitat required by animals (Van Dyck, 2012). Additionally, restoration practices aimed at improving habitat for one species may have a negative impact on another. For example, populations of a critically endangered lizard were found to be in decline following afforestation efforts (Hawlena *et al.*, 2010). By erecting metal poles to mimic the perches provided by trees, Hawlena *et al.* (2010) showed that increased avian predation of the lizards was caused by the novel addition of perches (i.e. the trees) in restored areas, a cue not recognised by the lizards due to the rarity of perches in their natural habitat. Although afforested habitats may be beneficial for perching birds, as emigrating lizards showed no preference for either restored or natural areas, afforested habitats effectively functioned as equal-preference ecological traps for the lizards, with significant impacts on population persistence (Hawlena *et al.*, 2010).

Despite a paucity of data on habitat preferences, many altered wetlands, including those discussed here, are likely at significant risk of functioning as ecological traps. Wetlands altered by agriculture, mining, restoration and urbanisation often superficially resemble natural wetlands and thus often contain the cues used by animals to select habitat. However, the often-high level of contaminants within these wetlands likely reduces habitat quality, but at levels potentially imperceptible to animals. As a result, the cues these wetlands contain are no longer accurate indicators of habitat quality (Hale *et al.*, 2015a). As such, ecological traps may form from the decoupling of habitat quality and preference, and we provide several lines of evidence that altered wetlands may function as ecological traps. For example, animal populations were often highly comparable between altered and reference (presumed to be higher-quality) wetlands. Although making the assertion that population size and habitat preference are intrinsically linked is inherently problematic as discussed

above, this finding, coupled with clear fitness reductions within these wetlands, provides some evidence that these sites have the potential to function as ecological traps.

The time elapsed since habitat alteration may play an important role in how animal communities and populations are structured within wetland systems (Norton, Evans & Warren, 2016). For example, newly created wetlands can be initially colonised by the endangered growling grass frog *Litoria raniformis*, but populations often decline through time (Koehler, Gilmore & Newell, 2014). Such situations may be indicative of the presence of an ecological trap, particularly if these altered wetlands continually receive, but do not supply, migrants. Conversely, newly created and altered wetlands may be initially unsuitable until vegetation matures or inhabitants adjust to human selection pressures (e.g. urbanisation; Evans *et al.*, 2010). Although the data required to incorporate a temporal component in our models were largely unavailable, future research and current management would benefit from such analyses. We suggest that researchers strive to include accurate information on the time elapsed since habitat alteration, and that ecological-trap research in particular monitors temporal variability in population sizes and habitat preferences. Quantifying temporal trends will enhance our knowledge of the trajectories of degradation (agriculture, mining and urbanisation) and recovery (restoration) and clarify our understanding of broader ecological principles, such as population dynamics, community assemblage formation and overall ecosystem function (Lake, Bond & Reich, 2007).

A comprehensive understanding of animal habitat preference is an important knowledge gap that may limit our capacity to manage altered wetlands. Creating and modifying wetlands to achieve an intended purpose while also providing suitable habitat for wildlife in concert will likely fail if habitat quality and animal preferences are not linked. Hale & Swearer (2017) propose ways to mitigate the potential for restoration activities to create traps, and ways to modify restored habitats to eliminate traps already formed. These guidelines could easily be adopted when dealing with wetlands utilised for, or otherwise impacted by, agriculture, mining and urbanisation. The authors suggest that in addition to focusing on resource-based, functional habitat approaches, ecologists and conservationists employ cognitive theory to incorporate information on how animals perceive and ultimately select habitats. We need to define clearly what represents habitat quality from the perspective of animals, gain a greater understanding of the underlying mechanisms of habitat selection, and determine how these factors could be manipulated.

Recently, an iterative framework to identify and manage ecological traps in aquatic systems has been proposed that applies and adapts knowledge of the principles of stream restoration and effective monitoring-program design (Hale *et al.*, 2015a). This involves addressing the evidence required to demonstrate an ecological trap; animals must prefer or equally prefer a habitat that confers lower fitness than other available habitats. Consequently, monitoring

individual fitness and, if necessary, testing if poor-quality habitats are preferred, will aid strategies to mitigate ecological traps if they are present. Gaining a greater understanding of the mechanisms that lead to animals preferring low-quality habitats, and the situations most likely to result in trap formation will aid the effective management and conservation of wetland-dependent animals.

V. IMPLICATIONS AND RECOMMENDATIONS

Although our meta-analysis highlights important generalities of wetland-associated animal responses to key drivers of environmental change, we caution against indiscriminately applying these results to all wetland systems affected by one of the drivers analysed here. As is common with many meta-analyses of ecological data, there is inherent variability in, and limitations of, the data used to estimate broad-scale responses. In addition, given our intentionally biased searching of the agricultural literature on amphibians, coupled with our selective use of search terms, we do not claim this to be an all-inclusive, systematic review. Nonetheless, given that our search term returned more than 30000 titles and we further obtained studies from review bibliographies, our meta-analysis provides a representative and comprehensive quantitative evaluation of the available literature. Meta-analyses are a powerful tool to discern overall trends, and here we have provided detailed summaries of taxon-specific responses to wetlands altered by agriculture, mining, restoration and urbanisation that can be used to guide future monitoring and management activities, and improve understanding of animal responses to environmental change.

Our review emphasises that the role of wetlands in human-altered ecosystems can be complex, with the potential that they are both important but also pose potential risks to animals. Dolny & Harabis (2012) suggest that the high biodiversity and presence of habitat specialists within altered wetlands is not coincidental, and that these habitats have significant conservation potential. Human-altered wetlands can provide different types of habitat to natural wetlands, increasing overall habitat heterogeneity, and the combination of wetland types likely provides resources for a greater number of species than natural wetlands alone. Given the ongoing destruction of natural wetlands, wetlands created for and impacted by humans will likely need to be an integral part of future natural resource management plans and conservation practices and policies.

However, we show that individual fitness may be severely compromised within these wetlands, and thus, there are inherent problems with using them for multi-objective management, where wetlands retain their primary function for human benefit and aim to provide suitable habitat for wildlife. Our findings also highlight the potential inadequacies of relying solely on community- and population-level measures as a proxy for habitat quality. The probable importance of altered wetlands for wildlife into

the future demands a greater understanding of how these habitats, and the contaminants found within them, affect the fitness of animals. We recommend monitoring more-sensitive fitness measures (e.g. survival and reproduction), with a focus on amphibians, prior to attempting to entice wildlife into altered wetlands.

In addition to increased efforts to quantify individual fitness, monitoring habitat preference has several further benefits. Firstly, identifying the capacity of animals to adaptively prefer and select higher-quality habitats will provide valuable information on the type of management or intervention required (Hale *et al.*, 2015a). For example, if animals are actively preferring low-quality sites, more effort will be needed to discourage settlement than if animals were actively avoiding these sites. Secondly, this knowledge may be used to mitigate the impact of low-quality wetlands by exploiting animal behaviour and habitat selection. By identifying the cues animals use to select habitats, we may be able to prevent them from utilising certain wetlands (e.g. removing host plants from low-quality wetlands that particular animals oviposit onto, such as the butterfly example discussed above; Severns, 2011). Conversely, we can manipulate environments to entice settlement by adding the cues used during habitat selection to high-quality wetlands. Clearly, these options require specific knowledge of animals' habitat preferences and the cues they use to select habitat, and given the current paucity of data available, these concepts remain largely unexplored (although see Robertson, 2012).

Ultimately, ecological monitoring and conservation efforts would gain from empirical studies that quantify individual fitness and habitat preferences. While time and financial constraints will likely impose considerable hurdles to the collection of complete information, robust temporal data will allow appropriate mitigation measures to be implemented when necessary, and are imperative to the long-term persistence of wildlife within altered wetlands. Given the potentially devastating consequences if some wetlands are functioning as ecological traps, there is an urgent need to investigate this phenomenon with controlled experiments to elucidate the mechanisms that lead to animals preferring low-quality habitats, and the environmental conditions most likely to result in wetlands functioning as ecological traps.

VI. CONCLUSIONS

(1) Wetlands are being altered, degraded and destroyed globally. Where animals inhabit wetlands altered by humans, some may provide vital habitat, whereas poor-quality wetlands could pose a considerable risk. This risk will be heightened if such wetlands are preferred over other available wetlands, and effectively function as ecological traps.

(2) We conducted a global meta-analysis to quantify and compare animal communities, populations and fitness within human-altered wetlands (i.e. those impacted by agriculture, mining, restoration and urbanisation) to those within reference wetlands. While animal communities and

populations within altered wetlands were similar to those in reference wetlands, fitness was often reduced within altered sites, albeit with substantial taxon- and driver-specific variability. Therefore, our review highlights the issue of wetlands in human-altered ecosystems insofar that they are potentially important habitats but also pose a considerable risk to animals.

(3) Amphibians in particular were highly susceptible to agriculture, mining and urbanisation, highlighting the possibility of using this taxon as an environmental indicator. While common fitness measures such as survival, reproduction and the prevalence of abnormalities were most affected, those related to metamorphosis, such time to and mass at metamorphosis, were unaffected. Consequently, measuring metamorphosis-related fitness proxies in isolation may not provide useful information on the quality of wetland habitats.

(4) Our review highlights the potential issue with focusing solely on community- and population-level metrics as a means of evaluating habitat quality. The paucity of data required to test for the possibility that altered wetlands are functioning as ecological traps warrants the integration of this theory into future monitoring programs. We need to define what represents habitat quality from the perspective of animals, and gain a greater understanding of the underlying mechanisms of habitat selection and how these factors could be manipulated. By doing so, we may identify previously unidentified conservation risks, as well as currently underappreciated habitats that can support animals and contribute migrants to other habitats despite suffering some level of ecological degradation.

(5) Reductions in the availability of natural wetlands means that altered wetlands are becoming more and more important to many aquatic animals. Given the potential for these wetlands to reduce the fitness of animals, strategies to enhance their quality and suitability should be implemented to maximise their conservation potential.

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Asterisks indicate references included in the meta-analysis.

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IX. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. Data extracted from the studies and subsequently used in the analyses.

Appendix S2. R code for all analyses with model structure and summaries provided.

Figure S1. Funnel plot showing the relationship between log response ratio (RR) estimates and study size (N_{total}).

Figure S2. Forest plot of response ratios (and their 95% CI on log scale) comparing amphibian fitness responses to

two different methods of assessing the impacts of agriculture (Applied and Not applied).

Table S1. The initial biological measures that data were extracted for, and the subsequent measures used in the meta-analysis.

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