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WETLAND RESTORATION

Wetland Conservation and Its Effects on Mosquito Populations

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Abstract

To stop the worldwide decline of wetlands, conservation measures like restoration, protection and construction of these ecosystems are indispensable. However, wetland conservation could influence mosquito populations. We analysed how conservation measures affect the species composition and abundance of mosquitoes by conducting a systematic literature review and generated results from 113 selected articles. Thereby, we separately assessed conservation measures in constructed, for example polders, and natural, non-constructed, wetlands. An increase in overall mosquito abundance was more prevalent in constructed wetlands, but not in studies conducted in non-constructed wetlands. Besides assessing overall mosquito abundance, we developed a scheme to rank mosquito species-specific nuisance after conservation measures. Mosquito species can differ in their nuisance potential according to their biting and host-seeking behaviors. We further assessed the effects of mosquito management practices on specific mosquito species and discussed different practices between constructed and non-constructed wetlands. Whereas in constructed wetlands more management practices could be applied, practices in non-constructed wetlands were limited. In conclusion, we were not able to reject entirely the hypothesis that mosquito populations change after conservation measures in wetlands.

Keywords Culicidae · Mosquito · Wetland · Floodplain · Marsh · Restoration

Zusammenfassung

Meist beabsichtigt man mit Naturschutzmaßnahmen degradierte Feuchtgebiete wieder zu vernässen. Dadurch entstehen häufig eine Vielzahl von Stillgewässern, welche potenziell auch von Stechmücken (Diptera: Culicidae) als Bruthabitate verwendet werden können. Wir haben eine weltweite systematische Literaturrecherche durchgeführt mit dem Ziel, die Effekte von Naturschutzmaßnahmen in Feuchtgebieten auf die Entwicklung und Abundanz von Stechmücken zu untersuchen. Hierzu haben wir die Ergebnisse von 113 Artikeln ausgewertet. Wir haben die Feuchtgebiete in zwei Kategorien unterteilt: natürliche und naturnahe Feuchtgebiete und konstruierte beziehungsweise neu erbaute Feuchtgebiete, zum Beispiel Regenrückhaltebecken. Bei der letzten Kategorie beobachteten wir, dass die generelle Abundanz der Stechmücken nach den Maßnahmen angestiegen ist, wohingegen in natürlichen und naturnahen Feuchtgebieten die Abundanz der Stechmücken gesunken ist. Darüber hinaus haben wir ein Schema zur Messung der Stechmückenbelästigung nach den Naturschutzmaßnahmen entwickelt. Aufgrund unserer geringen Stichprobengröße können wir jedoch keine eindeutigen Tendenzen in der Belästigung entdecken. Zusätzlich haben wir die Maßnahmen zur Stechmückenkontrolle in Feuchtgebieten evaluiert. Während in künstlich angelegten Feuchtgebieten eine Vielzahl von Kontrolloptionen angewandt werden kann, insbesondere vor Beginn der baulichen Maßnahmen, sind die Möglichkeiten in natürlichen und naturnahen Feuchtgebieten reduziert. Insgesamt können wir die Hypothese, dass die Stechmückenanzahl nach Naturschutzmaßnahmen in Feuchtgebieten ansteigt, nicht komplett verwerfen.

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Introduction

Over the past century, wetlands decreased globally. Davidson (2014) estimated a reduction of 62% to 75% of inland and coastal wetlands worldwide since 1900. Up to 89% of all the inland wetlands are not protected (Reis et al. 2017). Especially in densely populated areas, solutions are vital to sustain wetlands in the next centuries (for example Ramsar Convention on Wetlands 2021). Many national and international laws oblige states and actors in water management to conduct conservation measures in wetlands, i. e. restore, protect and construct wetlands. Conservation in these ecosystems is based on rewetting wetlands. Rewetting can generate stagnant water pools, which provide habitats for mosquito immatures (Willott 2004; Medlock and Vaux 2015a). Since mosquitoes are associated as nuisance and carriers of infectious pathogens (Medlock and Leach 2015), wetland conservation can result in public concerns (Willott 2004; Collier et al. 2016). Even if the likelihood of increased public health risks is low, the public concerns might result in mosquito control measures applied by authorities (Knight et al. 2003). Mosquito control, which is based on insecticides or habitat alterations, for instance impoundments, should be tailored locally with the minimum of possible side effects on the wetland ecosystem (Beketov et al. 2010; Dale and Knight 2012). However, a systematic mosquito control may interfere with conservation goals (Batzer and Resh 1992). Non-target organisms might be affected (Poulin 2012). If mosquito control is necessary due to nuisance or health risks, approaches that combine mosquito and wetland management might be beneficial (Dale and Knight 2008). Therefore, knowledge about present mosquito species, their nuisance potential and effects of wetland conservation on mosquitoes is important.

A growing body of literature has addressed the topic of wetland conservation and its influence on mosquitoes. Most research was conducted in Australia and USA focusing on management practices for marshes and constructed wetlands. Many articles addressed the Integrated Mosquito Management approach (IMM). In IMM the reduction of mosquito breeding habitats, the promotion of the native biota and educating the public are the main goals (Jackson et al. 2009; Walton et al. 2016, 2020; Martinou et al. 2020). IMM is considered an ecologically sound mosquito management practice in wetlands that includes the surveillance of mosquitoes and mosquito-borne pathogens (Rey et al. 2012). In intertidal marshes, studies proposed Open Marsh Water Management (OMWM), Rotational Impoundment Management (RIM) and runneling as promising practices. These management practices aim to control mosquitoes by favoring conditions for mosquito predators and simultaneously decreasing the amount of suitable mosquito breeding habitats (Carlson et al. 1991; Dale et al. 2014; Knight et al. 2021). The term runneling was used among others by Hulsman et al. (1989). Runnels are shallow spoon-shaped channels. These channels connect a system of salt marsh pools and follow natural water flow routes. In Europe, studies of Medlock and Vaux (2014, 2015a, b) addressed wetlands in the UK and Schäfer et al. (2004, 2006) studied wetlands in Sweden. Medlock and Vaux (2014, 2015a, b) observed how water level fluctuations could increase mosquito numbers. Schäfer et al. (2004, 2006) addressed natural and constructed wetlands and noticed that the older constructed wetlands did not facilitated higher number of mosquitoes compared to the natural wetlands. Authors also examined the topic in secondary research articles. One of the earliest reviews about wetland conservation and mosquitoes was written by Carlson et al. (1991) about salt marshes in Florida and the authors advised RIM to control mosquitoes. One of the most recent literature reviews concluded that wetland construction could enhance West Nile virus (WNV) infections (Medlock et al. 2018). WNV is transmitted by mosquitoes and can induce severe courses in birds, horses and humans (Apperson et al. 2004; Ziegler et al. 2019, 2020; Pietsch et al. 2020). Further, Beehler et al. (2021) did a comparative research study about wetland conservation cases. Involving mosquito control professionals in the Pacific Northwest of the USA from the beginning of the wetland conservation project can help to mitigate time and resources (Beehler et al. 2021). Verdonschot and Besse-Lototskaya (2014) reviewed systematically flight ranges of mosquitoes and discussed buffer zones for constructed wetlands. Besides the species-specific flight ranges, mosquito species differ in their habitat preferences, selection of breeding sites, biting and host-seeking behaviors (Becker et al. 2020). Mosquito species could also vary in their response to conservation measures in wetlands (Medlock and Vaux 2015b). Even though the medical relevance of mosquitoes is an important aspect of conservation projects, we decided to exclude this topic in our review. The mere mosquito species data is not sufficient to assess the risk of mosquito-borne pathogen transmission. Other environmental variables, for instance host availability and temperature, determine the effect of pathogenic diseases (Hubálek 2008).

The objective of our systematic literature review was to analyse if conservation measures in wetlands affect the species composition and abundance of mosquitoes. We evaluated how this topic is represented in scientific studies. We appraised the generated results of studies worldwide on whether overall mosquito abundance has changed. We expected different responses in overall mosquito abundance between constructed, for example polders, and natural, non-constructed, wetlands. Besides overall mosquito abundance, we also assessed to what extent conservation measures in wetlands intensify mosquito nuisance. We further classified and discussed mentioned management practices of the selected articles, to outline when and which practice could work and neither benefits mosquitoes nor ensues negative side effects. We assumed that there are different management practices in constructed and non-constructed wetlands. Throughout this article, the term '*mosquito management practices*' refers to strategies to control mosquitoes in wetlands.

Methods

Systematic Literature Search

We reviewed articles based on the PRISMA guidelines for '*transparent reporting of systematic reviews and meta-analyses*' (Panic et al. 2013). We structured our search into three components: type of wetland (subject), conservation measure (intervention) and effects of this intervention (outcome). The following search string was used: (bog* OR fen* OR floodplain* OR freshwater* OR lake* OR marsh* OR peatland* OR riparian* OR river* OR swamp* OR "wet meadow" OR wetland*) AND (conserv* OR construct* OR manag* OR preserv* OR protect* OR renat* OR restor* OR rewet* OR revital*) AND (culicid* OR diptera* OR mosquito* OR nuisance*). "Wet meadow" was in quotation marks to search for the entire term. The condition "NOT author" was added for the variables bog* and fen* in all three databases. The search string was applied in *Web of Science* and *PubMed* for all fields. In the database *Scopus*, the first two components, which structured our search (subject and intervention), were applied for title, abstract and keywords. The third component (outcome) was applied in *Scopus* for all fields. We covered the period from 1960 until 2021 in this systematic review. We chose 1960 because it was the earliest possible year in the database *Scopus*. In the screening process, we comprised references, when they were written in English, published in peer-reviewed journals and integrated all three components, which structured our search. In the screening of full texts, we omitted references, when they were based solely on mosquito control, impacts of mosquito control, mosquito ecology, wetland restoration and arthropod-borne viruses research. Literature results were organized in Endnote X9 (Clarivate Analytics, The Endnote Team 2013). We visualized graphics in RStudio 4.1.2 (RStudio Team 2021) with additional packages *readxl* (Wickham and Bryan 2022), stringr (Wickham and RStudio 2022) and *ggplot2* (Wickham 2016). In this review, we use the term conservation measures for restoration, protection and construction of wetlands. Generally, wetland restoration aims at reestablishing the original hydrology and expanding wetlands (Wagner et al. 2007). In inland wetlands, this could be done by artificial flooding of wetlands (Batzer and Resh 1992) to restore a natural flooding regime (Jacups et al. 2012). In coastal areas, the aim is to reconnect the marsh to the sea and intensify tidal flooding by digging tidal channels, or by OMWM, RIM or runneling (Turner and Streever 1999; Rochlin et al. 2009). The succession of degraded to near-natural habitats should also be achieved by protecting wetlands by law and preserving the remaining wetlands (Ortiz et al. 2005). While the construction of new wetlands has sometimes several purposes, we included studies, when wetlands were primarily constructed as habitats for wildlife (Sanford et al. 2003), for reconnecting separated wetlands (Schäfer et al. 2004), or for extending an existing wetland (Medlock and Vaux 2014).

Data Analyses

A total of 71 original research articles and 42 secondary research articles met the research criteria of our systematic literature review (see Supplementary Information Table S1). The 71 original research articles either assessed: (i) wetlands, in which conservation measures like restoration, protection and construction were applied ($N=47$), or (ii) wetlands, in which there was no application of such conservation measures and these wetlands were primarily considered as degraded ($N=19$), or (iii) laboratory experiments ($N=3$), or (iv) statistical models of field data ($N=2$) (for classification of articles into these four types see Supplementary Information Table S2). The original research articles about wetlands with conservation measures were differentiated in articles referring to studies conducted either in constructed ($N=21$) or non-constructed wetlands ($N=26$). Constructed wetlands have anthropogenic origins and initially did not exist, non-constructed wetlands are of natural origins (Kennedy and Mayer 2002; Knight et al. 2003). We refrained to further subdivide constructed and non-constructed wetlands, as information was not always given, and classification of wetlands is complex with different terms used for the same type (Dobson and Frid 2009).

Assessing Effects of Wetland Conservation on Overall Mosquito Abundance

To document the effects of conservation measures on mosquitoes, we chose overall mosquito abundance, since this was the smallest mutual factor of all articles. We evaluated the effects on overall mosquito abundance for 47 articles about constructed and non-constructed wetlands with conservation measures. We sorted the 47 articles' results about mosquito immatures and adults into: decrease, increase, no change, taxon specific responses, different responses of study sites, and no data on mosquito abundance. We chose to not assess the effects on overall mosquito abundance for studies based merely on wetlands with no conservational activities, laboratory experiments and statistical models. We focused on field experiments in constructed and non-constructed wetlands. We decided to include two types of studies: in the first type, mosquitoes were sampled before and after conservation measures; in the second type, study sites were compared to reference sites. Either wetlands with conservation activities were compared to wetlands with no conservation activities, or constructed wetlands were compared to non-constructed wetlands.

Evaluating Mosquito Species-Specific Nuisance Levels

Some mosquito species were described in original and secondary research articles as aggressive biters, e. g. *Aedes albopictus* (Unlu et al. 2021), or nuisance species, e. g. *Aedes vexans* (Becker et al. 2020). Aggressive or nuisance mosquito species are considered to occur in large numbers (Blomgren et al. 2018), can have more than one biting activity peak per day (Muhammad et al. 2020), and fly distances over two kilometers (Verdonschot and Besse-Lototskaya 2014). Due to such species-specific biological traits, the perception of a conservation measure among the public is not only influenced by changes in overall mosquito abundance but could also be affected by changes in the mosquito species composition. Therefore, we developed a classification of mosquito species-specific nuisance levels and applied it to four examples, selected by the following criteria on articles about wetlands with conservation measures ($N=47$):

(1) We excluded studies, in which solely mosquito immatures were sampled. According to this criterion, we removed 29 articles of the 47 selected studies.
(2) The articles must present data on mosquito abundance. We omitted studies, in which there was no data on mosquito abundance. This criterion led to the further exclusion of seven articles.
(3) Articles must report a complete list of collected mosquito species. This list must contain species data of either pre- and post-conservation measures or a comparison of study sites to reference sites. Based on these three selection criteria, we had four remaining articles to work with.

In the next step, we calculated nuisance levels for all mosquito species collected in the four selected articles. We allotted nuisance levels to points: zero points = very low nuisance, one point = low nuisance, two points = moderate nuisance, three points = high nuisance and four points = very high nuisance. These points are based on the biological traits of each collected mosquito species in the four articles and their respective biting and host-seeking behaviors: (i) being anthropophilic (biting preferably humans), (ii) mostly occurring in high abundance, (iii) being a strong flyer, and (iv) being an aggressive biter or nuisance. With the information obtained from several original and secondary research articles about extensive mosquito species descriptions (see Supplementary Information Table S3), each mosquito species scored a point, when a biological trait was given (scores also in Supplementary Information Table S3). A biological trait was classified without a point when it was not mentioned in any reference or when contrasting behaviors were observed for a species. We excluded other traits that are also likely to influence a mosquito species' nuisance level like feeding indoors (endophagic), biting activities per day and number of generations per year, because we did not obtain thorough information for these traits in the literature. Thereby, we decided to include the trait being an aggressive biter or nuisance as compensation for the excluded traits. If a collected mosquito species is anthropophilic, is described in the literature as aggressive or nuisance, occurs in high abundance, but is not a strong flyer, it scored three points. If another species is anthropophilic, is described in the literature as aggressive or nuisance, occurs in high abundance and is a strong flyer, it scored four points. Mosquitoes determined to taxonomic complex only, e. g. of the *Anopheles crucians* complex, *Anopheles maculipennis* complex and *Culex pipiens* complex, were excluded, since in these complexes species-specific biting and host-seeking behaviors might differ. We excluded the species *Aedes hendersoni* because no further literature information was found.

Analysing Mosquito Management Practices

To analyse different management practices of mosquito control in constructed and non-constructed wetlands, we screened the articles for management practices and checked for which wetland type and mosquito species the practice can be applied to reduce mosquito nuisance. We chose to include all 113 articles for analysing management practices. We divided management practices into six groups: habitat design, habitat design in tidal wetlands, hydrological measures, vegetation removal, vegetation management and predators.

Results

The Current Base of Studies

Screening titles and abstracts according to the search terms yielded 347 records (Fig. 1, screening). Of these 347 articles, 113 articles met the criteria relevant to our analysis (Fig. 1, included). The oldest selected article was published in 1978, the most recent in 2021. The 113 articles differed in their study design, objective and outcome. Field studies in wetlands were presented in 66 of these 113 articles. These field studies were conducted in North America (37 studies), Australia and New Zealand (12 studies), Europe (six studies), Africa (five studies), South America (five studies) and Asia (one study).

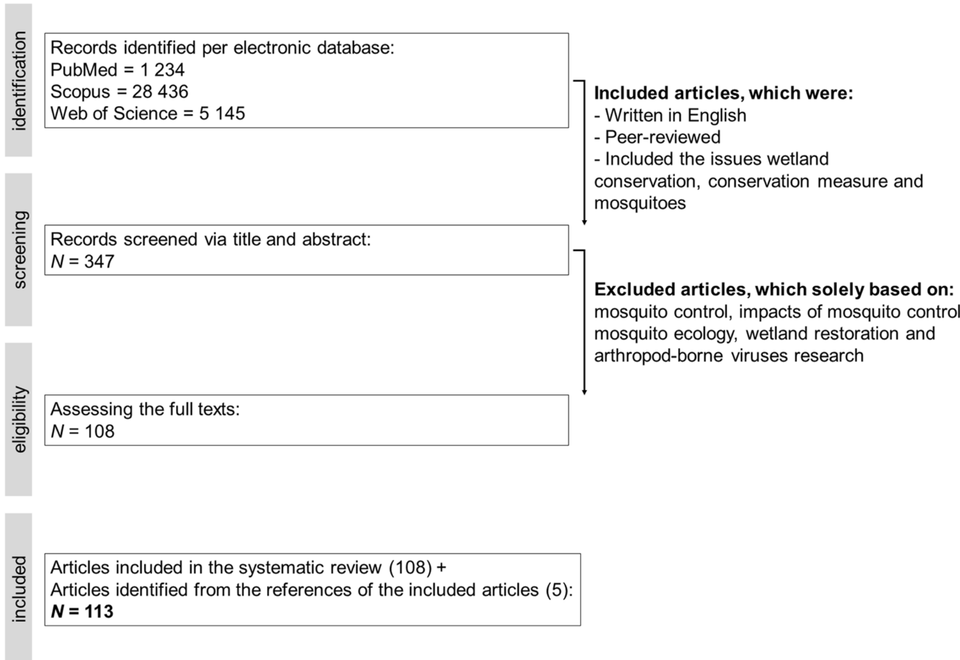

Fig. 1 Flow diagram illustration of the systematic literature search's quantitative outcome with the number (*N*) of articles, which met the criteria for each step (identification, screening, eligibility and included) and inclusion as well as exclusion criteria for the steps. Status of *N* = December 2021

Published Data on Effects of Wetland Conservation on Overall Mosquito Abundance

Based on our criteria (see Methods, Data analyses), we selected 47 studies to evaluate the effects of conservation on overall mosquito abundance (Fig. 2). We included 33 articles in Fig. 2, 17 referring to constructed and 16 to non-constructed wetlands. The remaining 14 articles belong to the category '*no data on mosquito abundance*' and were excluded. Most studies documented a decrease in overall mosquito abundance after the measures, with nine studies conducted in non-constructed wetlands and four studies in constructed wetlands. Another five studies, all addressing constructed wetlands, documented an increase in overall mosquito abundance after conservation measures. No change in overall mosquito abundance after conservation measures was observed in three studies, with two articles referring to non-constructed wetlands and one to constructed wetlands.

Nuisance Level Classification of Adult Mosquito Species

According to our criteria (see Methods, Data Analyses, Evaluating mosquito species-specific nuisance levels), we selected

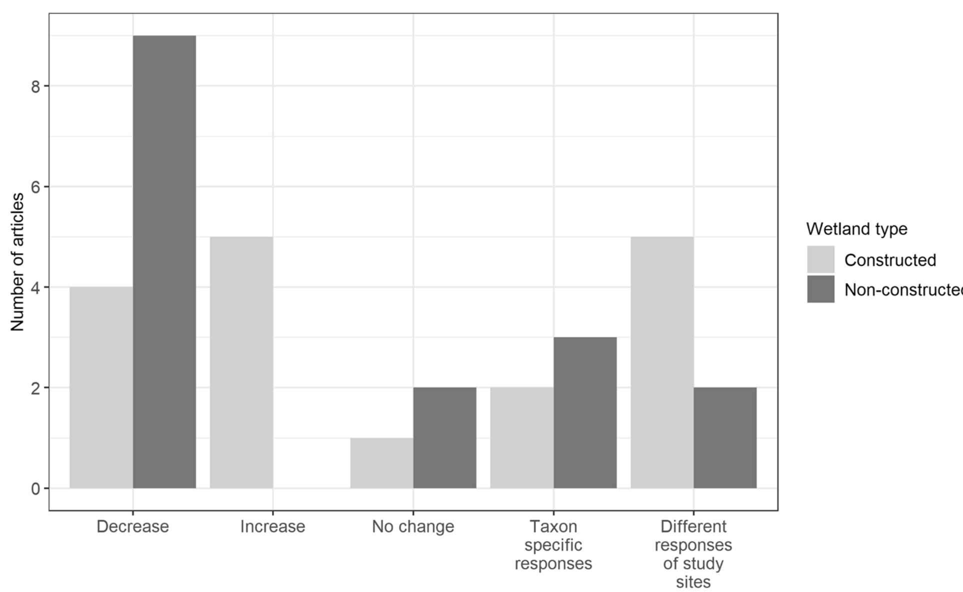

Fig. 2 Number of original research articles about constructed or non-constructed wetlands documenting effects of conservation measures on overall mosquito abundance. For a definition of conservation measures, which were included, see Methods, Systematic literature search. Effects on overall mosquito abundance were sorted into five categories: decrease, increase, no change, taxon specific responses and different responses of study sites. *N* of studies = 33

four studies as examples to apply our nuisance classification (Fig. 3). Across these four studies, a total of 76 mosquito species were collected. Based on our nuisance classification, ten of these 76 mosquito species were characterized by a very low nuisance level, 16 species were characterized by a low nuisance level, 20 species by a moderate nuisance, 21 by a high nuisance and nine as very high nuisance species (Fig. 3) (see Supplementary Information Table S3).

Management Practices to Control Mosquito Numbers and Nuisance

In 65 out of 113 articles, management practices to control mosquito numbers and nuisance in wetlands were presented (Table 1) (see Supplementary Information Table S4 for the 65 articles). While some articles did focus on one specific management practice, other articles addressed several measures to control mosquitoes. Habitat design was the most prevalent practice investigated in 40 articles, different vegetation control practices were studied in 25 articles, mosquito predators in 17 and hydrological measures in 16 articles (Table 1). We were able to define 22 mosquito management practices in the 65 articles (Table 1). We collected management practices for 46 mosquito taxa (Table 2). Most of the practices were primarily described for *Aedes* spp. species (Table 2).

Discussion

The goal of our systematic literature review was to evaluate to what extent conservation measures in wetlands affect mosquito populations. One aspect was to consider changes in overall mosquito abundance after conservation measures. Our results revealed that overall mosquito abundance decreased in non-constructed wetlands, but not in constructed wetlands. In these constructed wetlands, in which overall mosquito abundance increased, two out of the five studies sampled mosquitoes for at least two seasons (Anderson et al. 2007; Wagner et al. 2007). The remaining three studies collected mosquitoes in one season. These three studies included control areas to reduce the probability that seasonal and annual fluctuations in mosquito populations would influence the outcome of the study. Fleetwood et al. (1978) and Walton and Jiannino (2005) observed a significant increase in overall mosquito abundance. In the studied constructed wetlands from our review, authors often noticed an immediate rise in mosquito abundance after construction (for example Batzer and Wissinger 1996; de Szalay and Resh 2000; Schäfer et al. 2006; Anderson et al. 2007). Based on this trend throughout heterogeneous studies and study designs, we assume that the rise in mosquito abundance is more prevalent in constructed wetlands. Mosquitoes are rapid colonizers and adjust to a wide range of habitats (Becker et al. 2020). This might be a reason, why mosquitoes increased in constructed wetlands. A lack of potential predators as well as competitors in wetlands can also benefit mosquitoes (de Szalay and Resh 2000; Chase and Knight 2003). Managing constructed wetlands might induce higher mosquito numbers. For example, drawdown of water levels to clear decaying vegetation and then reflooding the wetland could increase mosquito immatures until predators are present (Batzer and Resh 1992; Sanford et al. 2003).

Even though overall mosquito abundance can deliver a first juxtaposition of the effects of conservation measures,

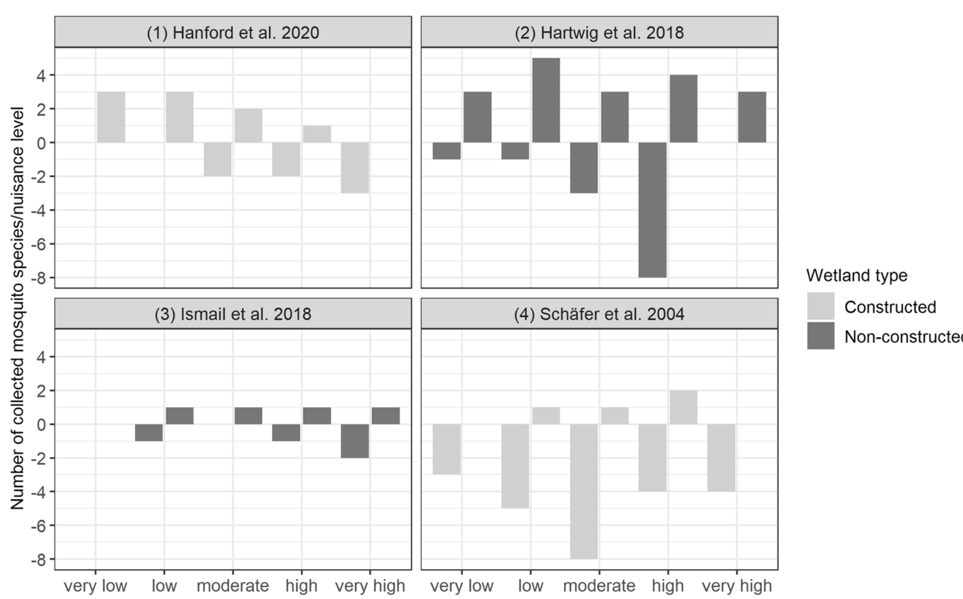

Fig. 3 Nuisance levels of collected mosquito species in four selected articles. The positive numbers show an increase in the collected mosquito species, while the negative numbers show that the species have decreased. *N* of collected mosquito species = 76

Table 1 From the selected articles mentioned management practices to control mosquito numbers and nuisance in constructed and non-constructed wetlands. Management practices are classified into six groups: Habitat design = HD, Habitat design in tidal wetlands = HDTW, Hydrological measures = HM, Vegetation removal = VR, Vegetation management = VM, Predators = P. Two practices are abbreviated: Open Marsh Water Management (OMWM), Rotational Impoundment Management (RIM). The number of articles for each management practice in a wetland type is given in brackets. '*Both*' means that the article addressed constructed and non-constructed wetlands for this practice. References are translated into numbers, for translation see Supplementary Information Table S4. $N = 65$ studies presenting management practices

Practice			
Groups	Details	Wetland type (# articles), practice was conducted in/advised for	Source
HD	Steep edges	Constructed (6)	5, 37, 41, 47, 48, 51
HD	Buffer zones	Constructed (4), non-constructed (3)	12, 27, 36, 37, 51, 57, 63
HD	Increasing water permanence	Constructed (4), both (1)	5, 6, 21, 54, 58
HD	Water depths	Constructed (4), non-constructed (3), both (3)	2, 5, 17, 26, 29, 30, 37, 47, 58, 65
HD	Open water zones	Constructed (5), non-constructed (1)	2, 5, 30, 41, 51, 54
HD	Connectivity and size	Both (5)	11, 18, 35, 37, 53
HDTW	Drainage ditches	Non-constructed (12)	5, 7, 9, 10, 28, 32, 33, 38, 40, 48, 55, 64
HDTW	Impoundments	Non-constructed (8)	7, 8, 9, 10, 19, 48, 58, 64
HDTW	OMWM	Non-constructed (11)	5, 7, 9, 14, 28, 31, 33, 38, 49, 56, 64
HDTW	RIM	Non-constructed (6)	7, 9, 10, 14, 38, 64
HDTW	Runnelling	Non-constructed (7)	5, 7, 14, 15, 28, 38, 48
HM	Flooding: time/season	Constructed (2), non-constructed (1), both (1)	43, 44, 45, 46
HM	Water level manipulations	Constructed (2)	37, 61
VR	Unspecified	Constructed (3), non-constructed (2), both (6)	4, 5, 20, 27, 42, 46, 47, 48, 61, 62, 65
VR	Burning of vegetation	Constructed (1), non-constructed (1), both (1)	22, 37, 48
VR	Mowing of vegetation	Constructed (4), non-constructed (3), both (2)	2, 16, 22, 34, 37, 39, 48, 52, 59
VM	Planting patterns	Constructed (1), both (1)	42, 60
P	Mosquitofish (invasive)	Constructed (3), both (4), laboratory (1)	5, 23, 24, 25, 37, 47, 48, 51
P	Native fish species	Constructed (1)	30
P	Beetles and true bugs	Constructed (2), non-constructed (2), both (1), laboratory (1)	1, 2, 3, 11, 13, 51
P	Dragonfly nymphs	Constructed (1), non-constructed (1), both (1)	5, 29, 51
P	Amphibians (frogs and salamanders)	Constructed (2), laboratory (1)	30, 50, 51

taking a closer look at the mosquito taxa could provide a better understanding of the impacts of conservation measures and nuisance. We, therefore, tried to assess changes in the mosquito nuisance after conservation measures. One mosquito species or genus might benefit from a conservation measure, while another species or genus might be disadvantaged. Medlock and Vaux (2015b) elaborated in their study in an English coastal wetland on the different habitat preferences of mosquito species and how they might react to wetland conservation measures. For instance, *Anopheles messeae* could increase when new open sunlit and permanent water bodies are created, while *Aedes rusticus* might benefit from wet woodland creation (Medlock and Vaux 2015b). We applied a nuisance classification because a perceived high nuisance among residents living close to conservation measures could hamper the conservation goals if systematic mosquito control is needed. Based on our criteria, we applied the nuisance classification to four articles. In these four articles high numbers of *Aedes* spp. were observed. Other articles studying constructed wetlands from our review collected high numbers of *Culex* spp. (Carlson and Knight 1987; Gingrich et al. 2006; Yadav et al. 2012). However, we excluded these articles from the nuisance classification, as they relied on the sampling of mosquito immatures. High numbers of immatures might not be reliable to indicate a high mosquito nuisance. Conclusions about the number of adult mosquitoes based on results of sampling mosquito immatures are difficult, since desiccation and precipitation influence the size of water bodies and thus the observed densities of the immatures (Service 1993). Additionally, survival rates of immatures might be varying among the four larvae stages and pupae, as Munga et al. (2007) observed in their study about *Anopheles gambiae* s.l. survival in semi-field experiments in Kenya. Consequently, we decided to only use data

Table 2 From the selected articles mentioned management practices to control specific mosquito taxa. Management practices are classified into six groups: Habitat design = HD, Habitat design in tidal wetlands = HDTW, Hydrological measures = HM, Vegetation removal = VR, Vegetation management = VM, Predators = P. One practice is abbreviated: Open Marsh Water Management (OMWM). The number of articles for each management practice in a wetland type is given in superscripts. References are translated into numbers, for translation see Supplementary Information Table S4

Taxa	Practice Group	Detailed practice + Source
Ae. albopictus	P	*Agabus punctatus* and *Agabus disintegratus*[13]
Ae. alternans	HD	Drainage[25]
Ae. annulipes/cantans	HM	In wet woodland slubbing of ditches[45,46], provide less shaded habitats[46]
Ae. canadaensis	HD + P	Increase water depths[50] + Increase numbers of larval salamanders[50]
Ae. cantator	HDTW	OMWM[33]
Ae. caspius	HM	Flooding of grasslands in late fall[45,46]
Ae. cinereus/geminus	HM + P	Flooding of reedbeds in winter[45,46] + Increase numbers of larval salamanders[50]
Ae. detritus	HDTW	Increasing tidal flooding of salt marshes[46]
Ae. dorsalis	HDTW	Restoring full tidal action[38]
Ae. melanimon	VR	50% plant cover[2]
Ae. notoscriptus	P	Dragonfly nymphs[29]
Ae. sollicitans	HDTW + HD	Increase tidal action[7,33,40] + Moderate to high shade (> 30% light reduction)[21]
Ae. taeniorhynchus	HDTW + VR	Increase tidal action[7,33] + Burning of vegetation[22]
Ae. vexans	HD + P	Moderate to low shade (< 90% light reduction)[21] + Increase numbers of larval salamanders[50]
Ae. vigilax	HDTW	Shallow runnels (< 0.3 m deep and 0.9 m wide)[15], drainage[25]
Anopheles spp.	P	Beetles and true bugs[13]
An. bancroftii	HDTW	Drainage[32]
An. bradleyi	HDTW	Drainage ditches and more tidal flushing[40]
An. claviger/petragagni	HM + VR	Ditches should have predators and competitors[46] + Maintain vegetation in ditches for sunlight[46]
An. farauti	HDTW	Drainage[32]
An. hermsi	VM	*Typha* sp. less *An. hermsi* than in plots with *Schoenoplectus californicus*[34], no mowing in fall[59]
An. punctipennis	HD + P	Moderate to low shade (< 90% light reduction)[21], increase water depths[50] + Increase numbers of larval salamanders[50]
An. vestitipennis	VR	Burning or mowing[22]
Coquillettidia spp.	VR	Removal[48]
Cq. perturbans	HD	Water level drawdowns occasionally[5]
Cq. richiardii	HM	In permanent habitats maintaining predator and competitor abundance in ditches[45]
Cq. xanthogaster	HDTW	Drainage[32]
Cs. incidens	VR	Removing of *Paspalum distichum*[39]
Cs. inornata	HD + VR	Lowest at 60 cm water depths[2] + Low vegetation coverage, mowing three weeks before flooding[16], removing of *Paspalum distichum*[39]
Cs. annulata	HM	No drying out of permanent ditches[45], flooding in summer[46]
Cs. melanura	P	Increase numbers of larval salamanders[50]
Culex spp.	HD + P	Increase wetlands' connectivity and predator abundance[11]
Cx. annulirostris	HD + P	Drainage[25,31,32] + *Gambusia holbrooki*[23]
Cx. coronator	VR	Burning of vegetation[22]
Cx. erythrothorax	HD	Continuous flooding[59]
Cx. pipiens s.l.	HD + VR	Moderate to high (> 30%) light reduction[21] + Removing of *Paspalum distichum*[39], cutting vegetation in flooded grassland[45,46]
Cx. quinquefasciatus	HD + VR	Drainage[25], continuous flooding[59] + Five weeks of vegetation drying then flooding[52] + Removing vegetation and then flooding[61] + Planting of *Bolboschoenus maritimus*[61]
Cx. salinarius	HD + HDTW	Low to moderate shade (< 90%)[21] + Drainage ditches and increased tidal flooding[40]
Cx. sitiens	HD	Drainage[25]
Cx. stigmatosoma	VR	Five weeks of vegetation drying then flooding[52]
Cx. tarsalis	HD + VR	Continuous flooding59, removing vegetation and then flooding[61] + Less vegetation[16] + If vegetation then *Typha* sp.[34] + Removing of *Paspalum distichum*[39] + Five weeks vegetation drying time[52] + Planting of *Bolboschoenus maritimus*[61]
Cx. territans	HD + P	Low to moderate shade (< 90%)[21] + Increase numbers of larval salamanders[50]

Table 2 (continued)

Taxa	Practice Group	Detailed practice + Source
Mansonia spp.	VR	Removal[48]
Ms. uniformis	HDTW	Drainage[32]
Ps. ferox	P	Increase numbers of larval salamanders[50]
Ur. sapphirina	HD	Low to moderate shade (<90%)[21]

of collected adult mosquitoes. Classifying nuisance based on mosquito species-specific biting and host-seeking behaviors has not yet been done in previously published literature.

Biting and host-seeking behavior can differ between the mosquito species and genera. For example, most *Aedes* spp. prefer to feed on mammals, including humans, whereas most *Culex* spp. have a more diverse host range, including mammals and birds (Börstler et al. 2016; Tomazatos et al. 2019). Therefore, concluding from the biting and host-seeking behaviors, *Aedes* spp. are more likely to cause greater nuisance than *Culex* spp. Marginal increases in high and very high nuisance mosquito species occurred in the studies of Hartwig et al. (2018) and Ismail et al. (2018) but decreased in the study of Schäfer et al. (2004) and Hanford et al. (2020). We assume that species-specific differences in response to certain habitat features might cause this effect. Hanford et al. (2020) observed a decrease in *Aedes alternans* and *Aedes vigilax* and an increase in *Aedes multiplex* and *Aedes procax*. According to our nuisance classification, *Ae. alternans* and *Ae. vigilax* are very high nuisance species, while *Ae. multiplex* is a very low nuisance species and *Ae. procax* is a low nuisance species. A comparable trend of species-specific reaction was evident in the study of Schäfer et al. (2004). We are aware that it is not possible to make conclusions about mosquito nuisance after conservation measures in wetlands with such a small study size and studies from all over the world with different ecologies. Therefore, the four studies shall only be seen as examples of how to implement our nuisance classification in practice. The classification is an attempt to value the mosquito species' capability to be a nuisance species and to compare the mosquito species with each other. How the species' nuisance is then perceived by the public depends on a variety of factors like sociodemographic and landscape factors (Brown et al. 2021). We wanted to stress with our nuisance classification that mosquito genera and species might react differently to the effects of conservation measures, subsequently influencing nuisance levels. Likewise, the success or failure of mosquito management practices might depend on present mosquito genera and species in a wetland.

We additionally analysed mosquito management practices by their wetland type and effects on specific mosquito species. We observed that many articles mentioned the surveillance of mosquitoes and mosquito-borne pathogens (Rey et al. 2012) as well as scaling mosquito nuisance for management practices (Martinou et al. 2020). This is also promoted by the Integrated Mosquito Management approach.

Medlock and Vaux (2014, 2015a, b) included mosquito species-specific knowledge in their studies about the time of flooding wetland habitats in the UK. Mosquito species vary in their phenology, wherefore hydrological measures like time of flooding has different outcomes on mosquito species. Flooding in early spring increased abundance of the moderate nuisance species *Ae. rusticus*, while the very high nuisance mosquito *Aedes detritus* decreased in density. Summer flooding facilitated the development of floodwater mosquitoes, such as *Aedes caspius* and *Aedes cinereus/geminus*, both high nuisance species. On the one hand, winter flooding caused a decrease in these floodwater mosquitoes. On the other hand, it increased numbers of the moderate nuisance species *Aedes annulipes/cantans* and high nuisance species *Aedes punctor*. Concluding from Medlock and Vaux's studies, adjusting seasonal flooding could be an option in wetlands to impede development of high and very high nuisance mosquitoes based on their phenology. As the observations of Medlock and Vaux were restricted to the mosquito fauna colonizing coastal wetlands in the UK, the outcome of management options will probably differ from wetland habitats and mosquito communities present in other regions.

This regional adaptation is likewise important for constructing buffer zones. Buffer zones between wetlands and residential areas can be a useful option to reduce mosquito nuisance (Verdonschot and Besse-Lototskaya 2014). Webb and Russell (2019) and Johnson et al. (2020) noted that buffer zones did not work in densely populated areas when strong-flying mosquito species are present. Adverse effects of increasing mosquito nuisance could be possible when buffer zones are designed wrong, for instance, Verdonschot and Besse-Lototskaya (2014) suggested that densely vegetated areas shall be avoided. Vegetation provides shelters for adult mosquitoes and could cluster temporary water bodies that are suitable habitats for mosquito immatures (Verdonschot and Besse-Lototskaya 2014). Mosquitoes follow these vegetated lines and could therefore be supported in their dispersal to the nearest village (Verdonschot and Besse-Lototskaya 2014). Landscape factors and present mosquito species must be considered (Verdonschot and Besse-Lototskaya 2014). Verdonschot and Besse-Lototskaya (2014) discussed the design of buffer zones in constructed wetlands, which can be adjusted according to the present mosquito species, their flight range and habitat preferences. Webb and Russell (2019) studied the dispersal of *Ae. vigilax* from natural mangroves into urban residential areas. They concluded that due to the strong flight range of *Ae. vigilax* a post-design of buffer zones might barely affect the dispersal and only mosquito species with a low flight range could be affected by buffer zones.

Many authors from the reviewed studies stated that it is easier to conduct management practice in constructed wetlands than in non-constructed wetlands since in constructed wetlands management practices can be planned before construction. In non-constructed wetlands, management practices must be chosen carefully, because there are many co-dependencies (Rey et al. 2012). Non-constructed wetlands are complex and interventions could have more negative environmental impacts than in constructed wetlands. The IMM approach advises to decrease breeding habitats for mosquitoes and to increase suitable conditions for mosquito predators (Walton et al. 2016, 2020; Martinou et al. 2020). Knowledge about mosquito habitat preferences could therefore help to decrease mosquito populations. For example, thickly vegetated areas proliferate habitats and food sources for mosquito immatures (Walton 2003). Increasing water depth, as hydrological measure, can reduce emergent plant growth. Conversely, shallow water zones can increase thickly vegetated areas, algae blooms and lower water quality. In constructed wetlands, where water depths can often be managed artificially, authors investigated the effect of various water depths on mosquitoes (Batzer and Resh 1992; Knight et al. 2003; Diemont 2006; Berg et al. 2010; O'Geen et al. 2010). These studies suggested depths from 0.2 to 1.5 m for mosquito control. Hood and Larson (2014) showed that beavers altered the non-constructed wetlands. Beavers dug channels, cut trees and deepened pools. The change into a more heterogeneous habitat had positive effects on other macroinvertebrates. Vegetation management could help to decrease mosquito populations and increase numbers of mosquito predators. Removing vegetation by burning or mowing can control mosquito numbers, although burning is usually not applied anymore nowadays. Concerning mosquito control, the negative side effects of vegetation removal can overweigh the benefits. Vegetation removal could decrease biodiversity, water quality, benefit invasive species and might release pollutants (de Szalay and Resh 2000; Grieco et al. 2005; Lawler et al. 2007). If there is no other option, removal in constructed wetlands can be advised by mowing. Malan et al. (2009) suggested building raised planting beds with surrounding deep-water zones in constructed wetlands in South Africa. Batzer and Resh (1992) compared 50% with 100% plant cover. They noticed that more mosquitoes declined in the 50:50 ratio of open and vegetated areas in constructed wetlands, while Chironomids and Dytiscids increased. The authors implied this observation might be because of higher oxygen levels and more wind attenuation, which would benefit Chironomids and Dytiscids, but not mosquito immatures.

Constructing more open water zones with less vegetated areas supports the presence of predators (Schäfer et al. 2006). The effects of predators on mosquitoes were investigated primarily in microcosms and laboratory experiments. Introducing non-native predatory species can have negative effects. The introduction of non-native mosquitofishes, *Gambusia affinis* and *Gambusia holbrooki*, were discussed in studies set in Sydney, Australia and California (Russell 1999; Van Dam and Walton 2007; Hanford et al. 2019a, b, 2020). These two mosquitofish species are highly invasive because of their productivity and they suppress native fish species. *G. holbrooki* was often introduced for mosquito control, especially in Australia, but was not effective, and is nowadays even prohibited in parts of Australia (The State of Queensland, Department of Agriculture and Fisheries 2019). Van Dam and Walton (2007) suggested that introducing mosquitofishes should be limited to regulated man-made habitats and isolated pools like impoundments, while in natural or connected habitats wetlands managers should rely on native fish species. For instance, in southern California the arroyo chub, *Gila orcutti*, (Van Dam and Walton 2007) or in Canada the three-spined stickleback, *Gasterosteus aculeatus* (Jackson et al. 2009). Interspecific competition might also reduce mosquito abundance. When predators are absent, interspecific competition can affect mosquito immatures. Elono et al. (2010) observed in temporary wetlands in Germany that mosquito immatures were negatively influenced by the presence of other invertebrates, as these invertebrates competed for resources with the mosquito immatures. Duquesne et al. (2011) detected harmful effects of cladocerans, *Daphnia magna*, on *Cx. pipiens* immatures in microcosms.

Habitat designs in tidal wetlands were addressed in 19 articles. Worldwide many humans live in coastal areas, therefore tidal wetlands are often studied when it comes to wetlands and mosquitoes (Haas-Stapleton and Rochlin 2022). One practice, applicable in these tidal wetlands, is digging drainage ditches. When drainage ditches are maintained properly, mosquitoes colonizing tidal wetlands can be controlled (Tonjes 2013) but creating drainage ditches implies cost-intensive maintenance. Some authors mentioned negative side effects of drainage ditches, e. g. loss of open water habitats and growth in non-marsh organisms (Hulsman et al. 1989; Wolfe 1996; Carlson 2006; Rey et al. 2012; Tonjes 2013). Impoundments, diked and flooded areas, can increase habitats for waterfowl and resident fishes (Carlson et al. 1991; Carlson 2006; Rey et al. 2012). Resident fishes complete all lifecycle stages within freshwater ecosystems and do not migrate into the ocean (U. S. Fish and Wildlife Service 2014). Impounded areas colonized by predatory fishes might control *Aedes* spp. populations (Wolfe 1996). Impounded areas could decrease biodiversity (Rey et al. 2012), destroy native vegetation (Carlson 2006) and degrade water quality (Rey et al. 2012). Rotational Impoundment Management (RIM) can circumvent these negative aspects. In RIM marshes are seasonally connected to the sea. Tidal circulation is done in winter, followed by complete flooding of the marsh during spring. Compared to impounded marshes, RIM provides better water quality, benefits salt-tolerant plants, marsh typical zooplankton and fish communities (Brockmeyer et al. 1997; Cianciotto et al. 2019). Besides RIM, OMWM is applied in previously ditched marshes principally along the east coast of the USA (Dale and Knight 2008). In OMWM, mosquito habitats are eliminated by digging ponds or shallow pools from 0.1 to 0.5 m deep. These ponds or pools are connected by channels. Flooding the marsh via channels provides access for predatory fishes (Rey et al. 2012). Nevertheless, OMWM can reduce marsh bird abundance, changes soil surface moisture and decrease water quality (Rey et al. 2012). Runneling is operated in Australia and adapted on the east coast of the USA (Raposa et al. 2019). Runnels shall mimic natural tidal channels and are 0.3 m deep and 0.9 m wide (Hulsman et al. 1989; Dale and Knight 2012). According to Hulsman et al. (1989), Dale and Knight (2012) and Rey et al. (2012) environmental impacts of runneling are minimal and benefit gastropods, crabs, prawns, fishes and natural marsh vegetation (Connolly 2005; Dale and Knight 2006). Knight et al. (2021) assessed long-term efficacy of runneling in Australia. The authors stated that maintenance is necessary for mosquito control. Degraded runnels blocked by vegetation, erosion or deposition should be newly dug.

In conclusion, a broad base of heterogeneous studies worldwide addresses the issue of wetland conservation and its effects on mosquito populations. While we observed an increase in overall mosquito abundance in constructed wetlands right after construction, we did not find an increase in overall mosquito abundance after conservation measures in non-constructed wetlands. Overall, management practices should be decided locally and based on wetland type and present mosquito species. Changes in mosquito abundance and species composition are possible after conservation measures but depend on several factors like wetland type, type of conservation measure and local mosquito species.

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Declarations

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