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Review

The Biodiversity of Water Mites That Prey on and Parasitize Mosquitoes

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Abstract: Water mites form one of the most biodiverse groups within the aquatic arachnid class. These freshwater macroinvertebrates are predators and parasites of the equally diverse nematocerous Dipterans, such as mosquitoes, and water mites are believed to have diversified as a result of these predatory and parasitic relationships. Through these two major biotic interactions, water mites have been found to greatly impact a variety of mosquito species. Although these predatory and parasitic interactions are important in aquatic ecology, very little is known about the diversity of water mites that interact with mosquitoes. In this paper, we review and update the past literature on the predatory and parasitic mite–mosquito relationships, update past records, discuss the biogeographic range of these interactions, and add our own recent findings on this topic conducted in habitats around the Laurentian Great Lakes. The possible impact on human health, along with the importance of water mite predator–prey dynamics in aquatic food webs, motivates an increase in future research on this aquatic predator and parasite and may reveal novel ecological functions that these parasitic and predator–prey relationships mediate.

Keywords: *Arrenurus*; *Lebertia quinquemaculosa*; Lake St. Clair Metropark; Belle Isle; Detroit; phoresy; mesocosm; Diptera; freshwater ecology

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1. Introduction

Water mites are both abundant and ubiquitous aquatic arachnids that are found globally in freshwater habitats, except in Antarctica. Water mites have high species richness and biomass and can easily be collected in the many habitats they occupy. Reports of over 600 specimens that represent up to 13 genera can be collected in under three hours in typical freshwater habitats in the Great Lakes region by using a basic dip net to collect aquatic debris, which, when placed on a white enamel pan, allows the mites to be easily siphoned by using a pipette, as they scurry out of the debris [1]. More recently, we reported 17 genera occupying one location in this region within the Detroit River [2]. A species accumulation curve from the Palearctic shows that a plateau in the curve has not been reached, indicating that many more species remain to be discovered [3]. Previous studies report that perhaps only half of water mite species in North America have been named, constituting around 6000 water mite species with potentially 10,000 or more species found globally [3]. In other regions of the world, such as the Neotropics, water mite biodiversity is largely unexplored, with species counts expected to be four times what is currently known [4]. Molecular barcoding has helped improve the knowledge of water mite diversity in North America, as is evident in our work in the Detroit River and Western Lake Erie, where we contributed several previously unknown molecular barcodes for multiple genera of water mites [2,5]. The high biodiversity attributed to water mites is thought to have been a result of repeated instances of rapid diversification that enabled exploitation of host insects such as Dipterans [6]. Some groups, such as *Lebertia*, are thought to have co-evolved with nematocerous Dipterans, such as chironomids, which are closely related to mosquitoes [6]. Subsequent sections in this review focus on the biodiversity of water mites that prey on mosquito eggs/larvae and parasitize emerging adults, with an emphasis on updating and correcting the known biodiversity, summarizing the biogeography, and identifying future research avenues with discussion of our recent findings.

Beyond the lack of knowledge about water mite biodiversity, studies on their life history strategies are also lacking, with virtually all previous reports of water mite diets based on laboratory observations. Water mites have a complex life cycle that has co-evolved with important freshwater insect groups, especially Diptera, including mosquitoes and midges [6], which have frequently, though not exclusively, been identified as water mite prey. Proctor and Pritchard [7] reviewed prey consumed by water mites, and their list included copepods, mosquito larvae, chironomid larvae, *Daphnia*, and ostracods [8–10]. This illustrates their importance as predators in aquatic habitats due to their widespread presence, voracious appetite, and high biomass [7]. Water mites are also important constituents of aquatic habitats due to their usefulness as bioindicator species of the habitats in which they are found [11]. Although this is a new area of investigation, studies in Central America and Europe have already shown the benefits of using water mites as bioindicators [12,13]. These studies underscore the importance of water mites in aquatic ecology and suggest the need for more investigation in water mite life history.

Water mite life history begins with a fertilized egg from which a larva hatches. Water mite larvae often develop into ectoparasites that parasitize aquatic insect adult hosts, such as mosquitoes, as the hosts eclose from their pupal case and enter an aerial environment. The host is used by the larval water mite for nutritional value and dispersal to a suitable habitat for post-larval development [6]. The effects of water mite parasitism on the host includes morphological damage and reduced survival and fecundity, therefore negatively affecting population sizes of host species if infection rates are high [6]. Almost two-thirds of host order species have been found to be in the order Diptera, which has been the main focus in studies of the effects of water mite parasitism [14]. After the parasitic larval stage, water mites detach from the host and develop into the deutonymph stage. During the deutonymph stage, water mites rapidly grow in body size mainly through predation on insect larvae, such as mosquito larvae, and other macroinvertebrates. Some water mite species, such as *Parathyas barbigera* and *P. stolli* have been found to prey on mosquito eggs in laboratory studies [15] and will be discussed later. Water mites subsequently develop into quiescent trytonymphs, and finally into predatory adult water mites. The presence of both parasitic and predatory behaviors and the combination of aquatic and terrestrial/aerial stages of water mites suggest that they may be important model species for understanding population dynamics of macroinvertebrate species that have a mix of aquatic and semi-aquatic life histories.

Mosquitoes have been more intensively studied than water mites, resulting in a more comprehensive understanding of their global biodiversity, comprising about 3500 species in at least 42 genera [16]. Mosquitoes have many predators and are considered an important food source for many aquatic organisms [16]. Mosquitoes have a semi-aquatic holometabolous life cycle that consists of four different stages—egg, larva, pupa, and adult [16]. The immature stages can exist in many types of aquatic habitats, allowing mosquitoes to have high species richness and biomass. Beyond inhabiting all types of permanent and ephemeral lentic and lotic freshwater habitats, mosquitoes are found to colonize rock holes, tree holes, parts of vegetation, and artificial containers, such as buckets, tires, flower vases, bird feeders, and more. The life cycle begins when fertilized eggs hatch into an aquatic larval stage and the larva typically hangs suspended from the water surface. The larva molts and sheds its skin, lasting for one to three weeks, depending on species type, water temperature, and food availability. The mosquito larval stage suffers the greatest threat of predation from aquatic species such as water mites. The pupa is a resting stage that is solely aquatic, with no feeding, and lasts from one to three days, during which the pupa metamorphoses into a flying adult that lives its life in both a terrestrial and aerial environment. The switching of adult mosquito hosts from animal to human can occur seasonally, enabling zoonotic disease transmission [16].

During the larval aquatic stage in the life history of mosquitoes, they are preyed upon by water mites. Water mites are true aquatic organisms, but many species (which are reviewed here) have an ectoparasitic larval stage that parasitizes organisms that may become airborne, such as mosquitoes. Biotic interactions, such as those of water mites and mosquitoes, contribute to functional biodiversity, which might be critical in sustaining ecosystems [17]. The impact of contemporary global biodiversity decline has prompted the United Nations (UN) to declare 2011 to 2020 as the "UN decade of biodiversity" [18]. Freshwater biodiversity is the most threatened form of biodiversity, and experts implore an increased investment in research and documentation of freshwater biodiversity [19].

Through the highly complex web of interactions among species, such as parasitism, ecosystem functioning and biodiversity can be altered [20]. One example of an ecosystem service provided by water mites includes lowering mosquito fecundity, and thus reducing mosquito prevalence [21–23]. These positive effects can be attributed to the presence of high diversity, because the likelihood of selection effects, facilitation from long-term coexistence, and niche complementarity are greater as diversity increases [20]. The ecosystem-level consequences from biodiversity loss are significant, being of the same magnitude as the effects on environments from other anthropogenic global-change stressors [24]. This reinforces the urgency of the conservation and restoration of biodiversity worldwide [25]. The importance of biodiversity can be demonstrated through several theories that link higher diversity to increased productivity, ecosystem stability, and resistance to invasion from exotic species [25].

Through the loss of biodiversity, we not only lose the species themselves, but we harm the direct and indirect community and ecosystem-level biotic interactions that they are embedded in, as well. Beyond just consumer diversity, the role of parasite diversity on ecosystem functions has rarely been regarded. Parasites are ubiquitous organisms that are capable of regulating host abundance and community assemblages, which in turn can impact host biodiversity and the ecosystem processes those hosts influence [20]. For example, a parasite that uses a herbivore host can reduce herbivore abundance, which can have a trophic cascade that increases plant primary productivity through reduced grazing pressure [26]. Parasites are capable of increasing or decreasing biodiversity through facilitating or removing novel traits, as well as increasing or decreasing trait diversity [20].

Water mites are globally diverse aquatic arachnids and increase the complexity of trophic networks by being both predators and parasites. This review updates our current knowledge of the diversity of water mites that interact with mosquitoes and updates past records. We summarize the literature on biogeography and discuss possible life history strategies of water mites. This work aims to advance water mite research by exploring new avenues of research revealed by preliminary data from mesocosm experiments regarding water mite predation on mosquito larvae in urban parks. Our mesocosm experiments reported here can be used to identify other water mite mosquito predators and could also be modified to study parasitism. This review also provides a platform to advance important aquatic ecological topics, such as predator–prey interactions and parasitism. The research on water mite parasitism and predation on mosquitoes remains a relevant area of investigation, given the many unknowns of the diversity of these biotic interactions and the continuing and ever-expanding threat from mosquitoes.

2. Materials and Methods

2.1. Literature Review

A literature review of all water mite associations with mosquitoes as predators and parasites, using the Wayne State University Web of Science© portal (Clarivate Analytics), resulted in 186 records from a total of 148,858,601 records. The search terms were "water mites parasite mosquito". A second search of "water mites predator mosquito" returned 24 records, of which none was relevant to the present review. A Google Scholar Publication search identified 41 records, comprising 2 books and 39 articles. Other articles of interest were obtained from primary authors themselves.

2.2. Field Experiments to Identify Water Mite Mosquito Predators

Mosquito-attracting mesocosms were deployed at 6 sites in Lake St. Clair Metropark (LSCMP), located in Harrison Township (42.5818° N, 82.8093° W), adjacent to Lake St. Clair, and at 6 sites in Belle Isle State Park (BI) (42.3433° N, 82.9743° W), a 400 acre urban island park in Detroit, MI, in the Detroit River, which forms the border between the United States and Canada (Figure 1). The mesocosms, consisting of buckets with a volume of 5 L suspended from wooden frames (Figure 2), were set up in wet-mesic flatwoods forest and marsh wetland habitats and monitored approximately every two weeks, from April through November 2018. The buckets filled naturally with rainwater, to varying depths, and by July, mosquitoes laid eggs in the buckets, and mosquito larvae were observed through October. After mosquito larvae were detected in the mesocosms, water mites (*Lebertia quinquemaculosa*, *Hydrachna*, or *Arrenurus*) were added to some mesocosms, at various intervals, while noting the presence or absence of mosquito eggs, larvae, and pupae at each interval (see Figure 2).

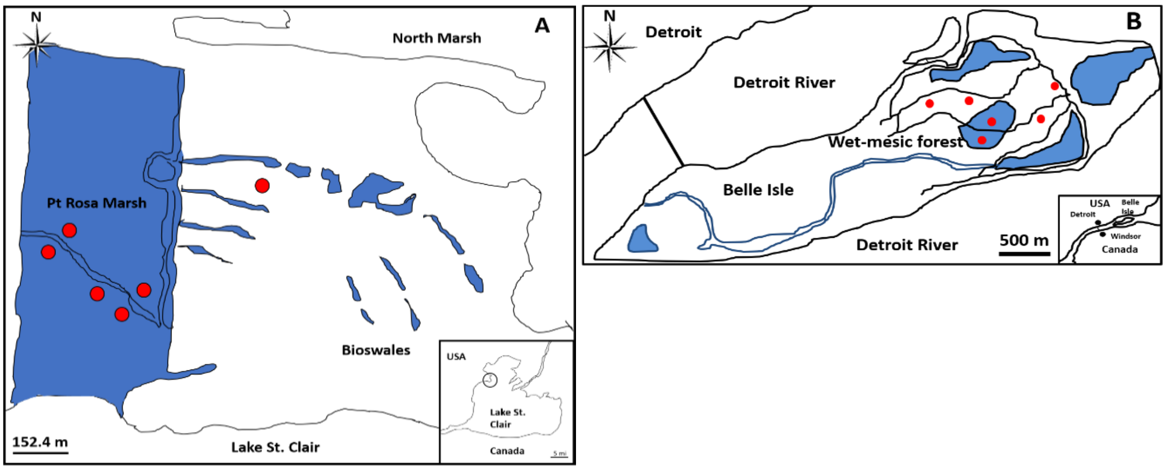

Figure 1. Maps of deployment sites (red markers) of mesocosm buckets. (**A**) Lake St. Clair Metropark; (**B**) Belle Isle State Park.

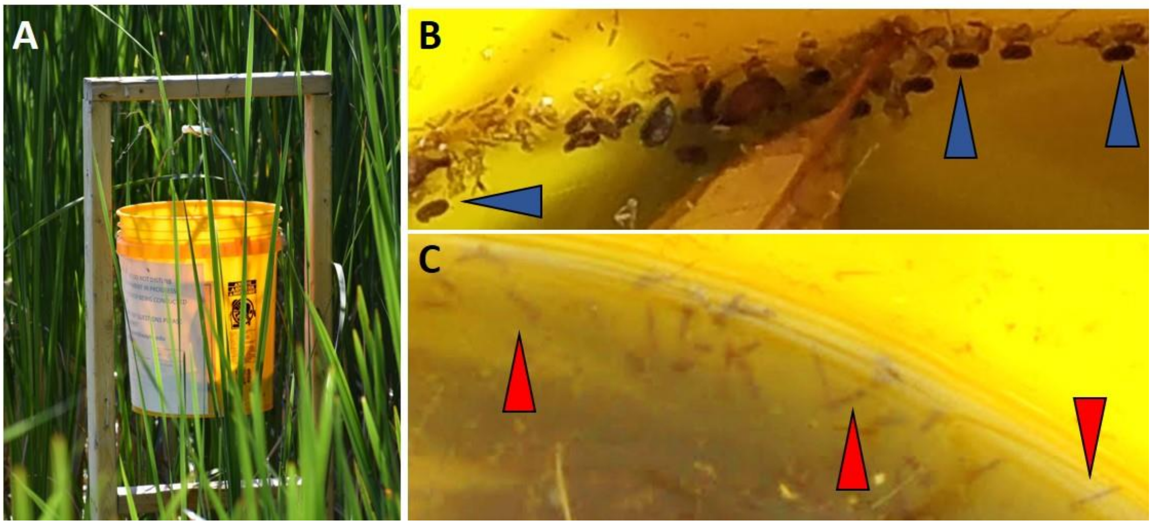

Figure 2. Mesocosms depicting mosquito larvae and pupae infestation. (**A**) Single-bucket mesocosm. (**B**) Mesocosm with mosquito pupae indicated by blue arrows. (**C**) Mesocosm with mosquito larvae indicated by red arrows.

3. Biodiversity of Water Mites and Mosquito Interactions

3.1. Predation

Since the 1700s, water mites have been studied by classical taxonomists such as Linnaeus and DeGeer. DeGeer (1778) reported water mite parasitism in his renowned work "Mémoires pour servir à l'histoire des insectes" (eight volumes, 1752–1778) [27]. However, observations of water mite predation on mosquito larvae were only reported much later, at the beginning of the 20th century. Water mites have been observed as predators of mosquito larvae under both natural conditions and controlled laboratory experiments. However, in comparison to the many studies of the diversity of water mites that parasitize mosquitoes, very few studies have been reported on the diversity of water mites as predators of mosquito larvae, eggs, or pupae. So far, there is only evidence of water mite predation on mosquito larvae and eggs, while there are no reports of predation on pupae. Smith [27] summarized the known material regarding mite predation of mosquitoes in his review, but there has been no update since then.

Here we discuss these previous observations and add six additional water mite records, since Smith [27], to the list of water mites that prey upon mosquito life stages (see Table 1). Mullen [15] observed *Thyas barbigera* and *T. stolli* preying on *Aedes* eggs in the laboratory. In that same work, he reported *Hydryphantes ruber* preying on *Aedes stimulans* larvae in the laboratory, and *Piona* feeding on mosquito larvae in woodland ponds. An earlier work by Laird observed *Limnesia jamurensis* feeding on *Culex pullus* and *Anopheles farauti* eggs and small larvae. They observed ponds devoid of mosquito larvae but filled with water mites and thus deduced that the mites might be the predators. They also conducted feeding experiments in the laboratory. Smith [27] also reported field observations of another water mite, *Piona,* feeding on mosquito larvae. Smith [27] suggested that adult *Arrenurus* mites feed on ostracods, while larval *Arrenurus* parasitize mosquitoes.

Table 1. Water mite impact on numbers of mosquito larvae in field-deployed mesocosms.

Mesocosm Identifier	Date Water Mite Added	Date Monitoring Mosquito Larvae
LSCMP#3	*Lebertia quinquemaculosa* 9 August 2018 Larvae present	No larvae observed 23 August 2018
LSCMP#2	*Hydrachna*, 31 August 2018 Larvae present	Larvae observed 7 September 2018
LSCMP#6	*Lebertia quinquemaculosa*, 11 October 2018 Larvae present	No larvae observed 19 October 2018
BI#6	*Lebertia quinquemaculosa* 15 September 18 and 17 October 2018, Pupae present, no larvae present	Pupae observed 22 October 2018
BI#3	*Arrenurus*, 15 September 2018 Larvae present	Periodically inspected no effect observed experiment ended 13 November 2018

Rajendran and Prasad [28] added a new taxon preying on mosquito larvae, *Encentridophorus similis* from the Unionicolidae family. Rajendran and Prasad [28] collected water mites of this species from adult mosquitoes and fed them *Aedes albopictus* larvae, which they preferred over copepods and ostracods. A subsequent study Rajendran and Prasad [29] provided the sole example of adult *Arrenurus* feeding on mosquito larvae. In experimental studies, *Arrenurus madaraszi* were fed larvae from *Aedes albopictus*, *A. hyrcanus*, and *A. vagus*. He noted that mosquito larvae became paralyzed when water mites attached themselves to the larvae. This suggests that water mites may be injecting venom that paralyzes the larvae, certainly a potential avenue for future research.

While Smith [27] mentions the work of Hearle [30], in which red water mites were observed to feed voraciously on mosquito "wrigglers" (larvae), known elsewhere as "wiggle waggles" (Pers comm. Belize colloquial use), he did not include it in his list. Perhaps this is because Hearle [30] did not identify the mite, although he wrote extensively on some life history characteristics where he kept mites and fed them. *Aedes vexans* larvae were provided upon which the mites then laid eggs that hatched after the season passed. Hearle [30] deduced that, in nature, the mites would lay eggs on leaves and debris and these would remain dormant until the following spring, at which point they would hatch. This observation has been confirmed in other mite species where seasonality is important in their life history. Smith [27] suggests that the mites observed by Hearle [30] were most likely *Piona*, which Smith [27] has also reported in his work as being predators of mosquito larvae. Bottger [31] had reported observations of *Teutonia cometes*, *Limnesia koenikei*, and *Hygrobates calliger* as preying on mosquito larvae, and although these were not included in the Smith [27] review of water mite predators of mosquitoes, these observations by Bottger were cited in the review by Proctor and Pritchard [7] on the scope of prey that water mites feed on.

Despite an estimated 57 families of water mites with 428 genera currently described [3], our current review observed only nine genera preying upon mosquito larvae or eggs (see Table 2). These observations include a new record, *Lebertia quinquemaculosa*, from our own study, described in this review (see Table 1). In this limited dataset, the addition of *Lebertia quinquemaculosa* to two mesocosms with mosquito larvae reduced the number of mosquito larvae to zero, whereas mosquito larvae continued to be present where *Hydrachna* and *Arrenurus* (see Table 1 and Figure 3) had been added. Interestingly, *L. quinquemaculosa* added to a mesocosm with only mosquito pupae present still had live pupae remaining when next inspected.

Table 2. The biodiversity of water mite predators of mosquitoes.

Family	Genus & Species	Mosquito Taxonomy and Prey Life Stage	Citation
Arrenuridae	*Arrenurus madaraszi*	*Anopheles* sp, *Armigerus* and *Aedes* sp larvae	[29]
Hydryphantidae	*Hydryphantes ruber*	*Aedes stimulans* larvae	[15]
Hydryphantidae	*Parathyas barbigera*	*Aedes* egg	[15]
Hydryphantidae	*Parathyas stolli*	*Aedes* egg	[15]
Hygrobatiidae	*Hygrobates calliger*	Unknown mosquito larvae	[31]
Lebertiidae	*Lebertia quinquemaculosa*	*Culex pipiens* larvae	This work
Limnesiidae	*Limnesia jamurensis*	*Anopheles farauti* and *Culex pullus* eggs and larvae	[32]
Limnesiidae	*Limnesia koenikei*	Unknown mosquito larvae	[31]
Pionidae	*Piona spp.*	*Aedes* larvae	[15,27]
Teutoniidae	*Teutonia cometes*	Unknown mosquito larvae	[31]
Unionicolidae	*Encentridophorus similis*	*Aedes albopictus* larvae	[28]

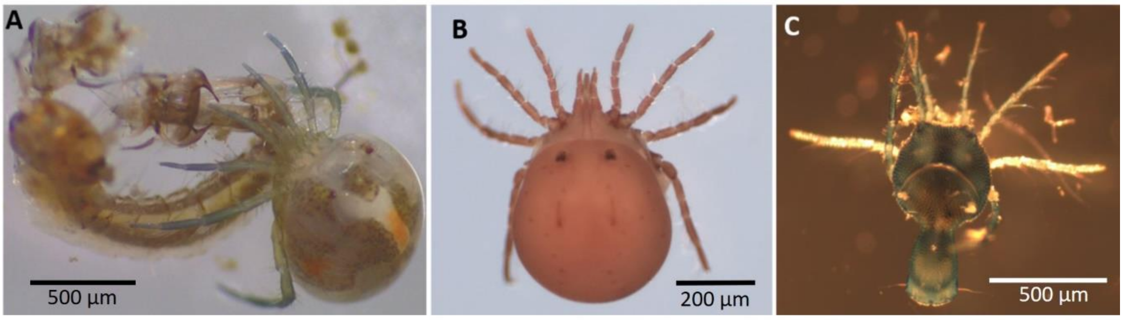

Figure 3. Micrographs of representative water mites used in mesocosms experiments: (**A**) *Lebertia quinquemaculosa* seen consuming a *Culex pipiens* larvae; (**B**) *Hydrachna* (ventral view), and (**C**) *Arrenurus* (ventral view).

3.2. Parasitism

Parasitism of mosquitoes by water mites was first recorded by DeGeer in 1778 and has since been an interesting focus of research for water mite investigators and others [27,33]. Comprehensive reviews of water mite parasitism on mosquitoes by Mullen [33] and Simmons and Hutchinson [34] revealed a global biodiversity of water mites that parasitize mosquitoes. The early work by Mullen [33] reported 15 genera of water mites that parasitize mosquitoes, but he disqualified five based on what he thinks were misidentifications or other inconsistencies. Smith [27] reported 10 genera mainly based on Mullen's work but not including the genera Mullen disqualified. Smith and Oliver [35] compiled an excellent review of parasitic hosts of larval water mites and their work agrees with the water mite–mosquito associations reported here. A newer study by Simmons and Hutchinson [34] reported seven genera and two families of water mites that parasitize mosquitoes. Water mites that parasitize mosquito adults overlap with six water mite genera that prey upon mosquito larvae and eggs (see Discussion). The mosquito hosts are similarly diverse, with 12 genera of mosquitoes having been identified by Simmons and Hutchinson [34]. In the present review, we add newer studies of water mites that parasitize mosquitoes; Table 3 lists the newer cases of water mite parasitism on mosquitoes that update the work since Simmons and Hutchinson [34].

Table 3. List of water mite–mosquito associations since Simmons and Hutchinson [34].

Parasitic Mite Taxa		Host Mosquito Taxa	Citation
Genus	**Species**		
Arrenurus	*acuminatus*	*Aedes pallidostriatus*, *Aedes pipersalatus*, *Anopheles barbirostris*, *Anopheles culicifacies*, *Anopheles minimus*, *Anopheles quinquefasciatis*, *Anopheles stephensi*, *Culex bitaeniorhynchus*, *Culex malayi*, *Culex nigropuntatus*, *Culex pipiens fatigans*	[36]
	danbyensis	*Culex infula*	[36]
	gibberifrons	*Aedes novalbopictus*	[36]
	kenki	*Aedes pallidostriatus*, *Aedes pipersalatus*,	[36]
		Anopheles quinquefasciatis, *Anopheles thomsoni*, *Culex malayi*, *Culex pipiens fatigans*, *Culex tritaeniorhynchus*, *Culex vishnui*, *Culex restuans*	[37]
	madaraszi	*Culex infula*	[36]
	spp.	*Aedes scapularis*, *Anopheles darlingi*, *Anopheles evansae*, *Psorophora ferox*, *Psorophora varipes*	[38]
Euthyas	spp.	*Culex restuans*	[37]
Hydrachna	spp.	*Aedes serratus*, *Mansonia wilsoni*,	[38]
		Psorophora varipes	[37]
Limnochares	spp.	*Aedes scapularis*, *Anopheles darlingi*	[37]
Parathyas	*barbigera*	*Aedes aegypti*, *Aedes albopictus*, *Aedes novalbopictus*,	[36]
		Aedes pallidostriatus, *Aedes pipersalatus*, *Aedes ramachandarai*, *Aedes vittatus*, *Anopheles barbarostris*, *Anopheles culicifacies*, *Anopheles minimus*, *Anopheles quinquefasciatis*, *Anopheles stephensi*, *Coquillettidia* spp., *Culex bitritaeniorhynchus*, *Culex infula*, *Culex malayi*, *Culex pipiens fatigans*, *Toxorhynchitis splendens*	[38]
	spp.	*Uranotaenia compestris* *Aedes albopictus*, *Aedes japonicus*, *Culex pipiens*, *Culex restuans*	[37]

Especially notable updates in Table 3 include observations by Atwa et al. [36], Manges et al. [37], and others. Atwa, Bilgrami and Al-Saggaf [36] reported new studies of water mites and their parasitic associations with mosquitoes, based on collections sourced in North India. Novel associations noted in this work included *Culex infula* associated with *Arrenurus danbyensis* and *Parathyas barbigera* [36]. Other *Culex* species, including *C. nigropuntatus*, *C. fatigans*, *C. malayi*, and *C. bitritaeniorhynchus* were reported associating with multiple *Arrenurus* genera, including *A. acuminatus*, *A. gibberifrons*, *A. madaraszi*, *A. kenki*, *A. danbyensis*, and *Parathyas barbigera* [36]. *Anopheles* genera also had new associations with *A. culcifactes*, *A. quinquefaciatis*, *A. stephensi*, *A. minimus*, and *A. barbarostris* with *Arrenurus* genera and *Parathyas barbigera* [36]. *Aedes* genera were also reported with new associations, including *A. albopictus*, *A. aegypti*, *A. pallidostriatus*, *A. pipersalatus*, *A. novalbopictus*, *A. vittatus*, and *A. ramachandarat* with *Arrenurus* genera. Likewise, *Parathyas barbigera* associated with *A. albopictus*, *A. aegypti*, *A. vittatus*, and *A. ramachandarat* [36]. Manges, Simmons, and Hutchinson [37] reported several new mosquito mite associations in North America, with mosquitoes that are considered invasive. *Aedes* genera, including *A. albopictus* and *A. japonicus*, were associated with *Parathyas* and *Culex restuands*, and *C. pipiens* were also associated with *Parathyas* [37]. Other interesting cases of parasitism, such as *Arrenurus* seen parasitizing a *Culex pipiens* pupae and *Unionicola* seen parasitizing a Cladoceran (*Bosmina tubicen*), are notable observations [38,39].

Our updated lists also include previously excluded data that should be considered, such as *Lebertia tauinsignata* reported by Marshall [40] but disqualified by Mullen [33]. We urge this reconsideration as we think *Lebertia tauinsignata* could possibly parasitize mosquitoes, as our own research shows *Lebertia* feeding on mosquito larvae and parasitizing chironomids, which are related to mosquitoes [10]. Our critical assessment of the work done by Marshall [40] did not find any reason to disqualify the observation. Another study that was disqualified by Mullen was the study by Mira [41] that identified *Unionicola* mites parasitizing *Anopheles* mosquitoes in what was Italian East Africa. Newer studies in the Arabian Peninsula adjacent to Ethiopia have identified *Unionicola* mites parasitizing mosquito pupae [38]. Other associations reported by Mullen [33] might need further assessment to determine why they were disqualified and if they should be considered again, given new research insights.

The *Arrenurus* genus commanded 61.67% of the parasitic associations, with 111 species of mosquitoes being parasitized (see Figure 4). The *Parathyas* genus was second highest, with 25.55% parasitic associations and 46 species of mosquitoes being parasitized. Further discussions on these two groups will be presented later, but it must be noted that the *Arrenurus* genera included several species of *Arrenurus*, but *Parathyas* was represented primarily by one species: *Parathyas barbigera*. In sum, the Arrenuridae water mite family (especially species of the genus *Arrenurus*) parasitized, by far, the greatest number of genera (11) and species (111) of mosquitoes (Figures 4 and 5). The water mite species and the number of mosquito species they parasitize are summarized in Figure 5. Within the *Arrenurus* genus, 27 species were found to parasitize mosquito larvae, with the most frequently observed species being *A. angustilimbatus*, *A. kenki*, and *A. madaraszi*. Since *Arrenurus* has the highest species richness of all water mite genera, and their larvae are generally difficult to identify at the species level, the diversity of *Arrenurus* species parasitizing mosquitoes may be even greater. Worldwide, 950 *Arrenurus* species have been documented [42], with 400 in the Nearctic region to date [6]. Newly assigned genera of water mites that parasitize mosquitoes included in the present review are *Lebertia* and *Unionicola*. These associations are based on our literature review, unpublished and published observations, and reassessment of previously rejected literature observations. For brevity, we did not include associations where the water mites could only be identified to family or subfamily taxonomic level, which included Euthyasinae and Thyadinae [34].

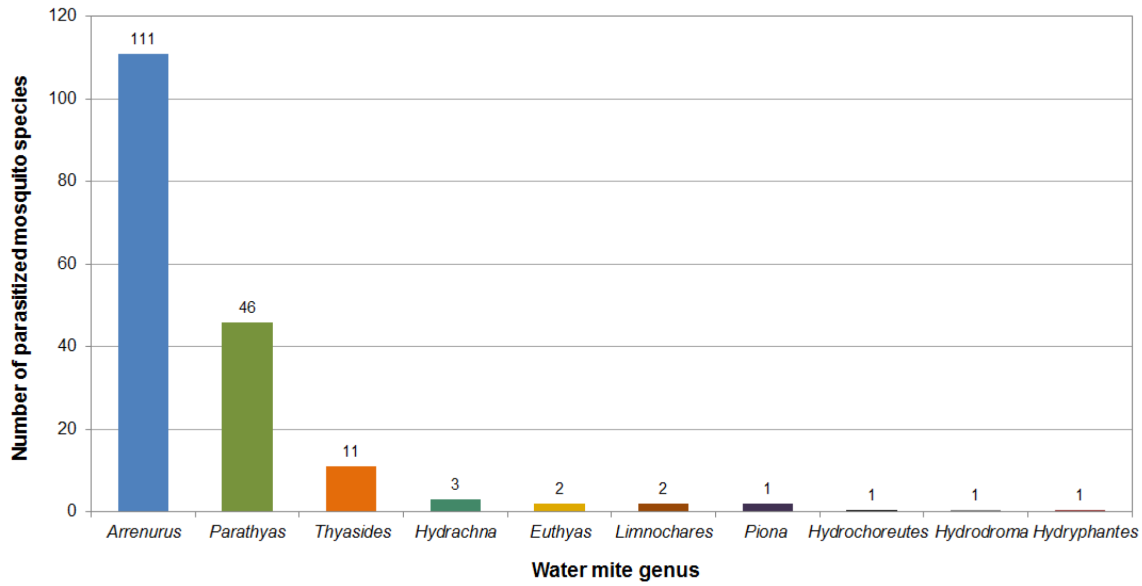

Figure 4. Number of parasitized mosquito species that are parasitized by each water mite genus, as reviewed by Atwa, Bilgrami, and Al-Saggaf [36]; Leal dos Santos [43]; Manges, Simmons, and Hutchinson [37]; and Simmons and Hutchinson [34].

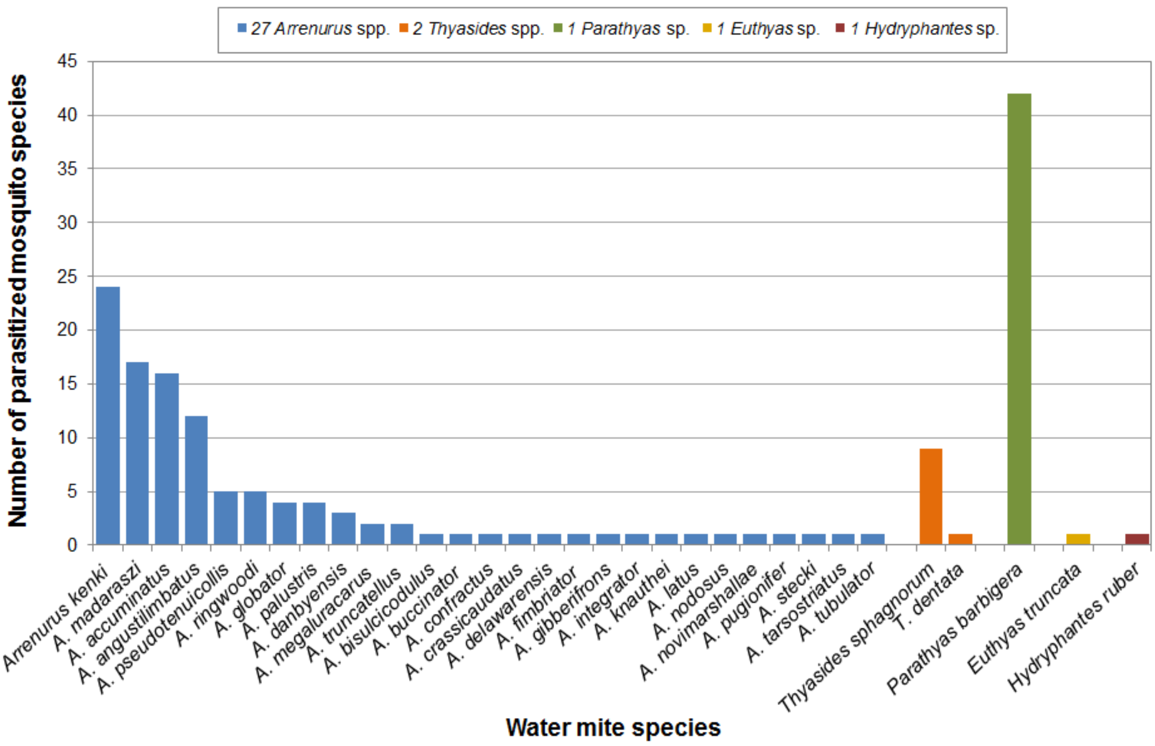

Figure 5. Water mites identified according to species and the number of mosquito species they parasitize, from Atwa, Bilgrami, and Al-Saggaf [36]; Leal dos Santos [43]; Manges, Simmons, and Hutchinson [37]; and Simmons and Hutchinson [34].

3.3. Global Perspectives and Considerations of the Biodiversity of Water Mite Predation and Parasitism of Mosquitoes

Despite Hydrachnidia (water mites) being the most biodiverse taxonomic group of the Arachnids, our analysis suggests that only about 3.5% of the total known water mite genera preys on and parasitize mosquitoes (see Table 4). However, some of the genera that have been shown to parasitize and prey on mosquitoes are believed to be some of the most specious, with *Piona* having potentially more than 100 species and *Arrenurus* up to 400 species [6].

Table 4. Overlap of water mite parasites and predators of mosquito adult and larvae, respectively.

Mite Genus	Mosquito Parasite	Mosquito Predator
Arrenurus	X	X
Encentridophorus		X
Euthyas	X	
Hydrachna	X	
Hydrochoreutes	X	
Hydrodroma	X	
Hydryphantes	X	X
Hygrobates		X
Lebertia	X [1]	X
Limnesia	X [1]	X
Limnochares	X	
Parathyas	X	X
Piona	X	X
Teutonia		X
Thyasides	X	

[1] Disqualified by Mullen, 1975 [33].

The aforementioned observations were based on both field and laboratory studies, comprising observations from the United States, Canada, Germany, Sweden, France, Denmark, New Zealand, Australia, Panama, Brazil, China, Japan, Uganda, Gambia, Madagascar, Nigeria, Angola, Indonesia, Malaysia, India, Sri Lanka, and Saudi Arabia (see Figure 6). While this demonstrates a broad global distribution of diverse water mite parasitism on mosquitoes, most reports originated from the United States and India, with over 100 records each.

Additionally, many biogeographical regions are left to be studied for water mite–mosquito associations, such as the Afrotropical and Neotropical regions, which are consequently known for mosquitoes and the diseases they cause (see Figure 6).

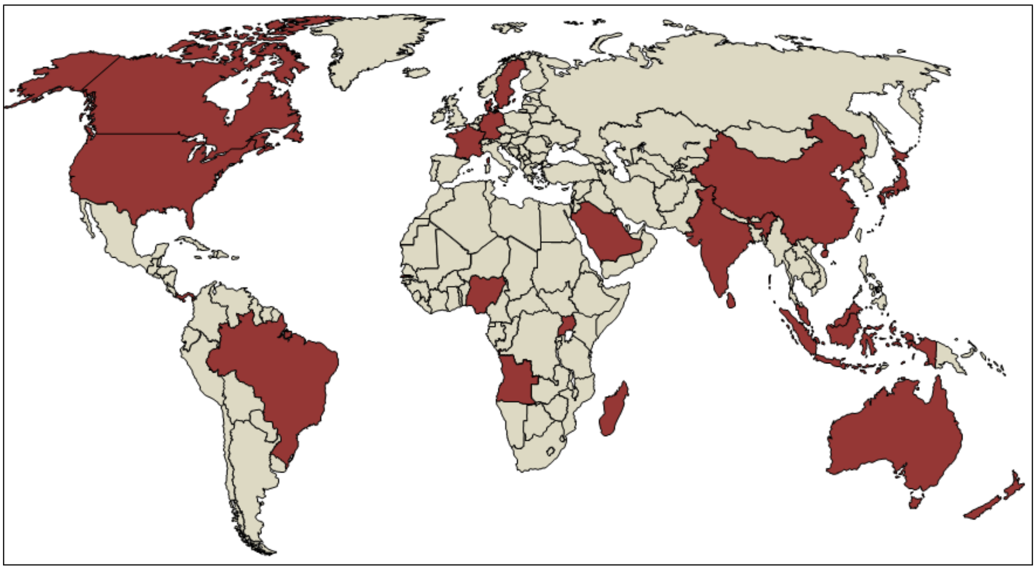

Figure 6. Map depicting locations (countries in red) where reports of water mite predatory and parasitic associations were obtained for this review.

4. Discussion

Water mites are known to be predators of a variety of aquatic invertebrates, including copepods, cladocerans, ostracods, and Dipteran larvae, and the larvae of water mites are also known to parasitize a diverse selection of invertebrates, such as dragonflies, mayflies, mosquitoes, and water beetles [7,35,44]. Given this diversity of biotic interactions they have as both predators and parasites, we consider their contribution to aquatic ecosystems to be very significant. The biodiversity of biotic interactions and the effect of parasitism on biodiversity are areas of research that are gaining renewed interest [17,20]. The specific aims of our work are to (i) update the known predatory and parasitic associations of water mites and mosquitoes (adults and larvae); (ii) update past records of water mite–mosquito associations; (iii) identify specific water mite genera and the biodiversity of their biotic interactions; and (iv) suggest future directions for studies with water mites, to increase our understanding of predatory biotic interactions in nature.

4.1. Identification of Major Water Mite Mosquito Parasites

Water mites are considered hyperparasites of mosquitoes, as they are a parasite that parasitizes another parasite, but despite these ecologically relevant biotic interactions, this area of research has been understudied [37,45]. Some mite species have been documented to parasitize multiple mosquito species throughout several genera, while other mite species have a very specific parasite–host association, with only a few mite species parasitizing a specific species of mosquito. Our review identified *Arrenurus kenki* as parasitizing 24 mosquito species of the genera *Aedes*, *Anopheles*, and *Culex* (see Table A1). Another water mite species that parasitizes a large number of mosquito species is *Parathyas barbigera*, which parasitizes 42 identified mosquito species in the genera *Aedes*, *Anopheles*, *Culex*, possibly *Coquillettidia* [46], *Psorophora*, *Toxorhynchitis*, and *Uranotaenia* (see Table A2).

The findings in our review suggest that the *Arrenurus* and *Parathyas* genus of water mites and their biotic interactions with mosquitos (as parasites of adult mosquitoes) might be an important area for future studies. *Arrenurus kenki* was listed as being "facultative tolerant" to organic wastes in a study that had a 0–5 range [47]. *Parathyas barbigera* (listed as *Thyas* in this reference) listed it as being facultative tolerant suggesting that both these species require an aquatic habitat that does not have excessive pollution [47]. This strengthens the idea that preserving biodiversity is important, especially in freshwater ecosystems that may contain these types of water mites which have a prominent role as mosquito parasites. It also emphasizes the loss of potential ecosystem services when the biodiversity of these biotic interactions is lost due to habitat loss or degradation. Work like this strengthens conservation efforts to improve freshwater habitats, since this is the habitat where biodiversity is disappearing at a faster rate than terrestrial systems [19].

4.2. The Potential Impact of Water Mite Life History Strategies on Their Biotic Interactions with Mosquitoes

Jalil and Mitchell [48] postulated that there are two types of water mites: the "thyasid-type", which belongs to the *Thyas* (=*Parathyas*) genus, and the "pionid-type", which includes those from the *Arrenurus* genus. In our review, the genera *Parathyas* and *Arrenurus* are those with the most significant parasitic associations with mosquito adult flies. The few studies focused on this topic have documented the possibility of water mite parasitism limiting the rate of survival and reproduction of mosquito hosts in natural environments to varying degrees [21,48–50]. The differing life history and behavior of thyasid-type and pionid-type mite larvae has previously been argued as playing a role in the attachment site and rate on mosquito hosts, and thus the intensity (as defined by the number of parasites on a host [51]) and severity of effects on mosquito survival and reproduction [48,49]. Thyasid-type mite larvae are believed to be closer relatives of terrestrial mites, from whom they evolved, than pionid-type larvae, because of their generalized, semi-aquatic life history [52]. Thyasid-type larvae are able to break through the water surface film immediately after hatching and "walk" on the water surface, having left the water altogether [48]. The thyasid-type larvae can only attach to adult mosquito hosts that return to the water surface, giving them only a few minutes of attack time to parasitize an adult mosquito host [49]. This may result in sexual discrimination by the thyasid-type mite larvae on female mosquitoes that exhibit a higher likelihood of returning to the water surface for oviposition of eggs than male mosquitoes [49]. In contrast, the pionid-type larvae are fully aquatic specialized swimmers that cannot leave the water until after they attach to the host. Therefore, pionid-type larvae can only seek a host during the mosquito's aquatic pupa stage, in which the mite larvae rest until mosquito ecdysis. After ecdysis of the mosquito pupa, the water mite remains on the adult mosquito, on which it initiates parasitism of the adult. This life history strategy may relate to the success in high intensity of mite parasitism with pionid-type larvae, specifically with *Arrenurus*, where *Arrenurus* mite load is commonly seen to be 30 or more mites per host [46,49]. Our review also identified *Arrenurus* as being the genus with the most species of *Arrenurus* parasitizing a wide diversity of mosquito hosts (see Figure 4 and Table A1).

Parathyas barbigera and *P. stolli* present an interesting case, as they were the second highest water mites having parasitic interactions with adult mosquitoes, with 42 different species of mosquitoes being parasitized by *P. barbigera* (see Figure 5 and Table A2). It was also found to prey on mosquito larvae (see Table 2). It was one of the few mites that had overlap with its larvae being parasites on mosquito adults and its adult form preying on mosquito larvae. This comparison can be seen in Table 4. *P. barbigera* and *P. stolli* belong to those water mites classified by Jalil and Mitchell [48] as "thyasid-type" mites, but despite this, they are very successful as predators and parasites of mosquitoes.

4.3. Water Mite Parasitism Reduces Mosquito Fecundity and Survivorship

The impact of high mite loads is evident from the linear relationship of mite-induced mortality and decreased fecundity on mosquito hosts, with the slope relating to the ratio of mite weight to host weight and the mite load on the host [22,50]. The few laboratory and natural experiments that have focused on the impact of high mite loads have commonly used the mite genus *Arrenurus* with the mosquito genus *Anopheles*, where reduced survivorship and reproduction of mosquitoes by *Arrenurus* species have been documented [21,23,50]. An experimental study by Lanciani and Boyt found that unparasitized female *Anopheles crucians* had a survival time of 23.32 days, while heavily parasitized females with *Arrenurus pseudotenuicollis* (around 17–32 mites) had a survival time of 6.25 days [21]. They also found that the number of eggs produced by *A. pseudotenuicollis* significantly decreased as *Arrenurus* mite load increased for both field-engorged mosquitoes and laboratory-fed mosquitoes, regardless of mosquito blood meal size [21]. Another experiment by Smith and McIver discovered that, when not accounting for blood meal size of *Coquillettidia perturbans*, the parasitism of *Arrenurus danbyensis* greater than five mites decreased the egg production of *C. perturbans* by 3.5 eggs per additional mite [23].

In a natural experiment by Lanciani and Boyt, the female *Anopheles crucians* that are unengorged with their first blood meal were found to have the highest proportion of pionid-type parasites compared to engorged female mosquitoes [21]. Another laboratory experiment by Lanciani discovered the sexual preference of *Arrenurus novimarshallae* mite larvae toward female *Anopheles crucians* pupae hosts compared to male pupae of that species, even when females were reared to smaller sizes with reduced food levels [53]. Female mosquitoes require sufficient energy to conduct flights for their required first blood meal to survive, but if they are heavily parasitized by pionid-type larvae, then they are most likely unable to attain this crucial blood meal, which can severely reduce mosquito densities.

Therefore, the effects and rates of parasitism by larval water mites and predation by deutonymph and adult water mites have been found to have a severe effect on population sizes of host and prey species. This, therefore, emphasizes the importance of future studies on loss of biodiversity of water mite parasitism and predation and the effects on the population size of species that they can potentially regulate. Since mosquito larvae have been found to be a possible host and prey for some species of water mites, it is crucial to determine the specific species of water mites that parasitize and prey on mosquito larvae.

4.4. Potential Water Mite Adaptations: Speciation and Niche Partitioning

We have also reviewed the water mites that have been shown to prey on mosquito larvae. Although the *Arrenurus* genus is substantially found to dominate the type of water mites that were found parasitizing mosquito adults (see Figures 4 and 5), we could only find one instance in which an *Arrenurus* adult water mite was found to prey on mosquito larvae in laboratory experiments (see Table 2) [29]. This demonstrates the hidden complexity within the biotic interactions since *Arrenurus madaraszi* was the only *Arrenurus* adult water mite found preying on mosquito larvae, but is the primary genus reported as parasitic (see Table 2 and Figure 5) [29].

Of the 17 genera listed, only six (*Parathyas*, *Piona*, *Hydryphantes*, *Arrenurus*, *Lebertia*, and *Limnesia)* were shown to both prey on and parasitize mosquito larvae and adults (see Table 4). Water mites are known to prey on and parasitize a wide variety of invertebrates. However, not all water mites are parasites. Up to 29 species are thought to not have parasitic larval stages, and studies that compare both parasitic and non-parasitic are needed to clarify possible adaptation benefits of one over the other [54]. A study comparing two species of *Arrenurus*, *A. angustilimbatus* (which is a parasite of mosquitoes and mentioned in this review) and *A. rufopyriformis* (which does not have a parasitic stage in its life cycle), concluded that *A. angustilimbatus* could be considered to be "ecologically successful" due to its higher heterozygosity and wide geographic range [55]. Studies on other species of water mites have also suggested species' separation as a consequence of parasitism [56]. Additionally, parasitic water mites have been observed to partition on a single host [57]. Up to nine water mite species were observed partitioning Chironomid hosts, with some species demonstrating preferred specificity to the thorax, while others to the abdomen [57]. This type of "niche" partitioning along with the phoresy associated with the parasitism of adult flies could contribute to the highly successful biodiversity and prevalence of water mites. However, due to poor taxonomy of water mites, particularly at the parasitic stage (larval stage), there is still much work needed to be done to fully appreciate the ecological and evolutionary contributions that these life history traits provide. However, with the ability for more accurate genus and species identification of water mites and mosquitoes via genetic analysis, and increased research on the abovementioned life history traits, an expanded understanding of these relationships will be made possible.

4.5. Biogeography of Water Mite–Mosquito Biotic Interactions

Because of the high species richness of both mites and mosquitoes and the extensive diversity of species-specific interactions between taxa, further investigation of the abundance of host exploitation and the effects of mite parasitism on mosquitoes seem likely to reveal a range of functional interactions. Even at the species level, these characteristics (attachment rate, mite load, and effects) of mite parasitism on mosquitoes have been previously found to vary depending on the species of both organisms involved in the parasitic interaction. Additionally, the biogeography related to these biotic interactions is also in need of clarification, since our overview of the biogeography of the groups discussed in this review could only be described at the family or subfamily level (see Table 5). Some of the genera have broad distribution, which may imply widespread impact through the diverse biotic interactions with mosquitoes. The cosmopolitan genus *Arrenurus* has published records of parasitism from widely distant regions, such as Japan and Canada, covering the Nearctic, Neotropical, Palearctic, Oriental, Australasian, and Afrotropical (see Table A3). More work is needed to understand the biodiversity, biogeography, and specificity of these biotic interactions, to document the extensive parasite–host association combinations that are present at a global scale.

Table 5. Biogeography of water mite genera.

Genus	Biogeography	Citation
Arrenurus	Cosmopolitan	[54]
Encentridophorus	Australasia, Asia, Africa	[54]
Euthyas	North America, Europe	[55,56]
Hydrachna	Cosmopolitan	[3]
Hydrochoreutes	Cosmopolitan	[54]
Hydrodroma	Cosmopolitan	[54]
Hydryphantes	Cosmopolitan, except New Zealand	[54]
Hygrobates	Cosmopolitan, except New Zealand	[54]
Lebertia	Cosmopolitan, except Australasian	[3]
Limnesia	Cosmopolitan	[3]
Limnochares	Cosmopolitan	[54]
Parathyas	Cosmopolitan family	[3]
Piona	Cosmopolitan	[54]
Teutonia	Holoarctic	[55]
Thyasides	Cosmopolitan family	[3]

4.6. Studies on Water Mite Predation of Mosquito Eggs, Larvae, and Pupae Are Needed

Similarly, with respect to predatory impacts of water mites on mosquitoes, further investigations are needed to determine ecological significance and, given the high health impact of mosquito-borne diseases, to determine if mite predation on mosquito larvae can be exploited to reduce these disease burdens. Commenting on the voraciousness of *Piona* spp. on mosquito larvae, Smith [27] noted that although *Piona* spp. are able to consume a large number of mosquito larvae, "quantitative studies on the ecology and feeding behavior of these mites are lacking", a statement that is still true almost 40 years later, as we write this review. A similar comment is made by Esteva et al. [58], who created a mathematical model of the roles of parasitism and predation in controlling the population dynamics of water mites and mosquitoes. The modelers observed in their model that predation had a more significant effect than parasitism in controlling the dynamics of mosquito and water mite populations. Indeed, in their model, populations of adult mosquitoes plummet to near zero as the water mite predation rate increases; the range of effective population-reducing predation occurs at a level of <0.9 mosquito larvae consumed per day per mite, which is a modest level compared to laboratory observed rates of six to eight mosquito larvae per mite by *Limnesia jamurensis* [32]. However, the modelers noted that "systematic studies about the extent of the impact of water mites on mosquito populations that could be used as a basis for a control program are scarce and fragmentary" [58].

Going forward, much new data needs to be collected on the intensity of water mite predation on mosquito larvae and about their impacts on mosquito populations. Our studies, reported elsewhere, applied high throughput sequencing to determine if mosquito DNA can be detected from the molecular gut contents of water mites freshly collected from the field [10]. The molecular gut contents from *Lebertia quinquemaculosa*, a second species of *Lebertia* with a novel COI barcode (tentatively named *Lebertia davidcooki*), and unidentified species of *Arrenurus* and *Limnesia,* was amplified with COI primers designed to amplify insects but not arachnids [10]. While DNA of many of the expected prey was present in these specimens (e.g., most sequences in *Lebertia* were from a multitude of chironomid species; *Arrenurus* had DNA from the ostracod *Podocopida*), sequences from mosquitoes were also present [10]. *Culex pipiens* sequences were observed in 20% of *L. quinquemaculosa* and 7% of *L. davidcooki* specimens, and neither of the other species [10]. We plan to apply these techniques to other water mite species, including *Piona*, which has figured prominently in this review of water mite–mosquito predation, to determine which, if any, species of water mites might utilize mosquito larvae as a predominant part of their diets. In addition, we have initiated mesocosm studies, reported here, to study water mite impacts on naturally recruited mosquito larvae (see Section 3.1).

These studies looked at naturally recruited mosquito larvae in aquatic mesocosms (see Figure 2) to which we have experimentally added water mites at various intervals. Our gut DNA studies in Vasquez [10] identified a potentially novel water mite mosquito predator, *Lebertia quinquemaculosa*, which we added to the mesocosms reported here. Mimicking "natural" artifacts, such as ponds and streams, vernal ponds, puddles, and other damp areas such as plant phytolemata [59], and also man-made water-retaining structures, such as cisterns, rain gutters, and buckets, we deployed bucket mesocosms in urban parks (see Figures 1 and 2), all of which provide an extensive range of mosquito-breeding habitats. Examples of such features in an urban area have been documented in Detroit [10] and are generally found in urban areas elsewhere [60,61]. We showed, in our results, that the addition of *L. quinquemaculosa* reduced mosquito larvae population in the mesocosms (see Table 1). We have thus added *L quinquemaculosa* to the list of water mite mosquito predators (see Table 2).

To our knowledge, these observations of water mite and mosquito larvae in bucket mesocosms constitute the first field test of its kind that investigated water mite impacts on mosquito populations in a naturalistic environment. On a preliminary basis, at least, *L. quinquemaculosa* seems to have a greater effect on mosquito larvae recruitment or survival than do two other genera of mites (*Arrenurus* and *Hydrachna*) which we added to our mesocosms (see Table 1 and Figure 3), a result supported by our molecular diet research on *Lebertia* and consistent with previous diet preference research on the other species [6,7,10]. As noted above, a systematic investigation of diverse water mite species, including those suggested to have predatory associations with mosquito larvae or eggs, would be warranted, especially to provide data for mathematical models of water mite–mosquito interactions and ultimately to determine whether water mite predation could be exploited to control mosquitoes. These mesocosm studies could also be enhanced with cameras and other observational methods that would clarify the mechanisms by which water mites impacted the recruitment, growth, and/or survival of the mosquito larvae in mesocosms.

5. Final Considerations

This knowledge of the functional biodiversity of water mites that feed on and parasitize mosquitoes could be of great importance in understanding predator–prey dynamics [20] and developing new methods for controlling mosquitoes. Several different types of diseases, such as West Nile virus, eastern equine encephalitis, dengue, malaria, Zika, yellow fever, and chikungunya, are caused by mosquitoes. The human morbidity due to mosquitoes is estimated at 725,000 worldwide, making it potentially the deadliest animal on earth (https://www.cdc.gov/globalhealth/stories/world-deadliest-animal.html). While our current research is in temperate regions where eastern equine encephalitis and West Nile virus are especially of concern, most mosquito-borne diseases of human pathological importance are primarily found in tropical regions, where, ironically, water mite biodiversity is least understood [4]. DNA barcoding could potentially assist in improving the knowledge of water mite diversity, since water mite adult and larvae DNA barcodes could be matched, thereby greatly facilitating research on mite–mosquito interactions [34].

Climate change and increased international travel provides an additional motivation for understanding water mite–mosquito interactions, as rising temperatures may allow organisms—such as mosquitoes—of the tropics to invade more temperate regions, posing new threats to human health [62]. Such changes may increase the financial burden for cities trying to control mosquito populations. As an example, expenditures for mosquito control in Miami-Dade County were recently at ten million dollars annually, five times its proposed budget (http://www.wlrn.org/post/miami-dade-county-faces-10-million-tab-mosquito-control). The Environmental Protection Agency (EPA) and the Centers for Disease Control (CDC) recommend an Integrated Pest Management (IPM) approach for the control of mosquitoes (https://www.epa.gov/mosquitocontrol/joint-statement-mosquito-control-united-states) that emphasizes natural control, with minimal chemical intervention when possible. Among these natural control methods may be the application of diverse species of water mites, as more natural biocontrol agents for mosquitoes, to reduce their human disease burden.

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Appendix A

Table A1. *Arrenurus* water mite species and the mosquito species they parasitize [34,36,37,43].

Parasitic Mite Taxa		**Host Mosquito Taxa**	
Genus	**Species**	**Genus**	**Species**
Arrenurus	*acuminatus*	*Aedes*	*pallidostriatus, pipersalatus*
		Anopheles	*barbirostris, culicifacies, minimus, punctipennis, quadrimaculatus, quinquefasciatis, stephensi, walkeri*
		Culex	*bitaeniorhynchus, malayi, nigropuntatus, pipiens, pipiens fatigans*
		Culiseta	*melanura*
	angustilimbatus	*Aedes*	*abserratus, aurifer, cinereus, communis, diantaeus, excrucians, fitchii, provocans, punctor, stimulans*

Table A1. *Cont.*

Parasitic Mite Taxa		Host Mosquito Taxa	
Genus	**Species**	**Genus**	**Species**
		Culex	*restuans*
		Culiseta	*morsitans*
	bisulcicodulus	*Anopheles*	*maculipennis*
	buccinator	*Anopheles*	*maculipennis*
	confractus	*Culex*	*restuans*
	crassicaudatus	*Anopheles*	*maculipennis*
	danbyensis	*Aedes*	*canadensis*
		Coquillettidia	*perturbans*
		Culex	*infula*
	delawarensis	*Coquillettidia*	*perturbans*
	fimbriator	*Anopheles*	*maculipennis*
	gibberifrons	*Aedes*	*novalbopictus*
	globator	*Aedes*	*excrucians*
		Anopheles	*claviger, maculipennis*
		Culex	*pipiens*
	integrator	*Anopheles*	*maculipennis*
	kenki	*Aedes*	*abserratus, canadensis, communis, excrucians, fitchii, japonicus, pallidostriatus, pipersalatus, provocans, punctor, stimulans, trivittatus, vexans*
		Anopheles	*quinquefasciatis, thomsoni, walker*
		Culex	*malayi, pipiens fatigans, restuans, restuans, salinarius, territans, tritaeniorhynchus, vishnui*

Table A1. *Cont.*

Parasitic Mite Taxa		Host Mosquito Taxa	
Genus	**Species**	**Genus**	**Species**
	knauthei	*Anopheles*	*maculipennis*
	latus	*Anopheles*	*maculipennis*
	madaraszi	*Anopheles*	*annularis, culicifacies, hyrcanus, nigerrimus, pulcherrimus, sinensis, stephensi, subpictus, vagus*
		Culex	*epidesmus, fuscophala, infula, pipiens fatigans, pseudovishnui, tritaeniorhynchus*
	megaluracarus	*Mansonia*	*uniformis*
		Anopheles	*walker*
		Culex	*territans*
	nodosus	*Anopheles*	*maculipennis*
	novimarshallae	*Anopheles*	*crucians*
	palustris	*Anopheles*	*walker*
		Culex	*restuans, territans*
	pseudotenuicollis	*Culiseta*	*morsitans*
		Aedes	*triseriatus*
		Anopheles	*crucians, punctipennis, quadrimaculatus, walker*
	pugionifer	*Anopheles*	*maculipennis*
	ringwoodi	*Aedes*	*trivattatus*
		Anopheles	*punctipennis*
	stecki	*Culex*	*restuans, salinarius, territans*
		Anopheles	*maculipennis*
		Culex	*pipiens*
	tubulator	*Anopheles*	*maculipennis*

Table A1. *Cont.*

Parasitic Mite Taxa		Host Mosquito Taxa	
Genus	**Species**	**Genus**	**Species**
		Anopheles	*aconitus, annulipes, aquasalis, barbirostris, costalis, coustani, darlingi, earlei, evansae, fluviatilis, gambiae, jamesi, karwari, maculatus, maculatus willmori, pallidus, philippinensis, punctipennis, ramsayi, splendidus, squamoses, sundaicus, tessellatus*
	spp.	*Coquillettidia*	*bitaeniorhynchus, crassipes, richiardii, venezulensis*
		Culex	*bitaeniorhynchus, brevipalpis, cornutus, erraticus, gelidus, malayi, modestus, pipiens, quinquefasciatus, sinensis, tarsalis, vishnui, whitmorei*
		Culicidae	spp.
		Culiseta	*alaskaensis, annulate, impatiens, inornata*
		Deinocerites	*atlanticus, melanophylum*
		Ficalbia	*chamberlaini*
		Mansonia	*annulifera, indiana*
		Psorophora	*ferox, varipes*
		Uranotaenia	*maculipleura*

Table A2. *Parathyas* water mite species and the mosquito species they parasitize [34,36–39].

Parasitic Mite Taxa		Host Mosquito Taxa	
Genus	**Species**	**Genus**	**Species**
Parathyas	*barbigera*	*Aedes*	*abserratus*, *aegypti*, *albopictus*, *annulipes*, *canadensis*, *cantans*, *cantator*, *caspius*, *cataphylla*, *cinereus*, *communis*, *detritus*, *excrucians*, *fitchii*, *idahoensis*, *leucomelas*, *novalbopictus*, *pallidostriatus*, *pipersalatus*, *provocans*, *punctor*, *ramachandarai*, *sticticus*, *stimulans*, *trichurus*, *triseriatus*, *trivittatus*, *vexans*, *vittatus*, *zoosuphus*
		Anopheles	*barbarostris*, *culicifacies*, *minimus*, *quinquefasciatis*, *stephensi*
		Coquillettidia	*perturbans*, sp.
		Culex	*bitritaeniorhynchus*, *infula*, *malayi*, *pipiens fatigans*
		Psorophora	sp.
		Toxorhynchitis	*splendens*
		Uranotaenia	*compestris*
	spp.	*Aedes*	*albopictus*, *japonicus*
		Culex	*pipiens*, *restuans*

Table A3. *Arrenurus* species biogeography.

Zoogeographic Region	Country	*Arrenurus* Species	Source
Nearctic	Canada	*angustilimbatus*	[34]
		kenki	[34]
		megaluracarus	[34]
		palustris	[34]
	USA	*acuminatus*	[34]
		angustilimbatus	[34]
		confractus	[34]
		danbyensis	[34]
		delawarensis	[34]
		globator	[34]
		kenki	[34,37]
		megaluracarus	[34]
		novimarshallae	[34]
		palustris	[34]
		pseudotenuicollis	[34]
		ringwoodi	[34]
		tarsostriatus	[34]
Neotropical	Brazil	spp.	[34,43]
	Panama	spp.	[33]
Palearctic	France	spp.	[34]
	Germany	*bisulcicodulus*	[33]
		buccinator	[33,34]
		crassicaudatus	[33]
		fimbriator	[33]
		globator	[33,34]
		integrator	[33]
		knauthei	[33]
		latus	[33]
		nodosus	[33]
		pugionifer	[33]
		stecki	[33]
		truncatellus	[33,34]
		tubulator	[33]
	China	*madaraszi*	[34]
	Japan	*madaraszi*	[33]

Table A3. *Cont.*

Zoogeographic Region	Country	*Arrenurus* Species	Source
Oriental	India	*acuminatus*	[36]
		danbyensis	[36]
		gibberifrons	[36]
		kenki	[36]
		madaraszi	[34,36]
	Indonesia	spp.	[34]
	Japan	*madaraszi*	[33]
Australasian	Australia	spp.	[34]
Afrotropical	Angola	spp.	[33]
	Madagascar	spp.	[33]
	Nigeria	spp.	[33]
	Saudi Arabia	spp.	[38]

References

1. Cook, D.R.; Mitchell, R.D. Notes on collecting water-mites. *Turtox News* **1953**, *30*, 122–125.
2. Vasquez, A.A.; Carmona-Galindo, V.; Qazazi, M.S.; Walker, X.N.; Ram, J.L. Water mite assemblages reveal diverse genera, novel DNA barcodes and transitional periods of intermediate disturbance. *Exp. Appl. Acarol.* **2020**. [CrossRef] [PubMed]
3. Di Sabatino, A.; Smit, H.; Gerecke, R.; Goldschmidt, T.; Matsumoto, N.; Cicolani, B. Global diversity of water mites (Acari, Hydrachnidia; Arachnida) in freshwater. *Hydrobiologia* **2008**, *595*, 303–315. [CrossRef]
4. Goldschmidt, T. *The Biodiversity of Neotropical Water Mites*; Springer: Dordrecht, The Netherlands, 2002; pp. 91–99.
5. Vasquez, A.A.; Qazazi, M.S.; Fisher, J.R.; Failla, A.J.; Rama, S.; Ram, J.L. New molecular barcodes of water mites (Trombidiformes: Hydrachnidiae) from the Toledo Harbor region of Western Lake Erie, USA, with first barcodes for *Krendowskia* (Krendowskiidae) and *Koenikea* (Unionicolidae). *Int. J. Acarol.* **2017**, *43*, 494–498. [CrossRef]
6. Smith, I.M.; Cook, D.R.; Smith, B.P. Water mites and other arachnids. In *Ecology and Classification of North American Freshwater Invertebrates*, 3rd ed.; Thorpe, J.H., Covich, A.P., Eds.; Academic Press: Waltham, MA, USA, 2010; pp. 485–586.
7. Proctor, H.; Pritchard, G. Neglected predators—water mites (acari, parasitengona, hydrachnellae) in fresh-water communities. *J. N. Am. Benthol. Soc.* **1989**, *8*, 100–111. [CrossRef]
8. Pozojevic, I.; Jursic, L.; Vuckovic, N.; Doric, V.; Gottstein, S.; Ternjej, I.; Mihaljevic, Z. Is the spatial distribution of lentic water mite assemblages (Acari: Hydrachnidia) governed by prey availability? *Exp. Appl. Acarol.* **2019**, *77*, 487–510. [CrossRef] [PubMed]
9. Matveev, V.F.; Martinez, C.C.; Frutos, S.M. Predatory—Prey Relationships in Sub-Tropical Zooplankton—Water Mite against Cladocerans in an Argentine Lake. *Oecologia* **1989**, *79*, 489–495. [CrossRef]
10. Vasquez, A.A. Digestive composition and physiology of water mites. Ph.D. Thesis, Wayne State University, Detroit, MI, USA, 2017.
11. Goldschmidt, T. Water mites (Acari, Hydrachnidia): Powerful but widely neglected bioindicators—A review. *Neotrop. Biodivers.* **2016**, *2*, 12–25. [CrossRef]
12. Goldschmidt, T.; Helson, J.E.; Williams, D.D. Ecology of water mite assemblages in Panama—First data on water mites (Acari, Hydrachnidia) as bioindicators in the assessment of biological integrity of neotropical streams. *Limnologica* **2016**, *59*, 63–77. [CrossRef]
13. Wiecek, M.; Martin, P.; Gabka, M. Distribution patterns and environmental correlates of water mites (Hydrachnidia, Acari) in peatland microhabitats. *Exp. Appl. Acarol.* **2013**, *61*, 147–160. [CrossRef]

14. Martin, P.; Gerecke, R. Diptera as hosts of water mite larvae—an interesting relationship with many open questions. *Lauterbornia* **2009**, *68*, 95–103.
15. Mullen, G.R. Predation by water mites (Acarina-Hydrachnellae) on immature stages of mosquitos. *Mosq. News* **1975**, *35*, 168–171.
16. Rueda, L.M. Global diversity of mosquitoes (Insecta:Diptera:Culicidae) in freshwater. *Hydrobiologia* **2008**, *595*, 477–487. [CrossRef]
17. Luna, P.; Corro, E.J.; Antoniazzi, R.; Dáttilo, W. Measuring and Linking the Missing Part of Biodiversity and Ecosystem Function: The Diversity of Biotic Interactions. *Diversity* **2020**, *12*, 86. [CrossRef]
18. United Nations Decade on Biodiversity. Available online: https://www.cbd.int/undb/goals/undb-unresolution.pdf (accessed on 2 May 2020).
19. Albert, J.S.; Destouni, G.; Duke-Sylvester, S.M.; Magurran, A.E.; Oberdorff, T.; Reis, R.E.; Winemiller, K.O.; Ripple, W.J. Scientists' warning to humanity on the freshwater biodiversity crisis. *Ambio* **2020**. [CrossRef]
20. Frainer, A.; McKie, B.G.; Amundsen, P.A.; Knudsen, R.; Lafferty, K.D. Parasitism and the Biodiversity-Functioning Relationship. *Trends Ecol. Evol.* **2018**, *33*, 260–268. [CrossRef]
21. Lanciani, C.; Boyt, A. Effect of a parasitic water mite, Arrenurus-Pseudotenuicollis (Acari-Hydrachnellae), on survival and reproduction of mosquito Anopheles-Crucians (Diptera-Culicidae). *J. Med. Entomol.* **1977**, *14*, 10–15. [CrossRef]
22. Smith, B. Host-parasite interaction and impact of larval water mites on insects. *Annu. Rev. Entomol.* **1988**, *33*, 487–507. [CrossRef]
23. Smith, B.; Mciver, S. The impact of *Arrenurus danbyensis* Mullen (Acari, prostigmata—Arrenuridae) on a population of *Coquillettidia perturbans* (Walker) (Diptera, Culicidae). *Can. J. Zool. Rev. Can. Zool.* **1984**, *62*, 1121–1134. [CrossRef]
24. Hooper, D.U.; Adair, E.C.; Cardinale, B.J.; Byrnes, J.E.K.; Hungate, B.A.; Matulich, K.L.; Gonzalez, A.; Duffy, J.E.; Gamfeldt, L.; O'Connor, M.I. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* **2012**, *486*, U105–U129. [CrossRef]
25. Tilman, D.; Isbell, F.; Cowles, J.M. Biodiversity and Ecosystem Functioning. In *Annual Review of Ecology, Evolution, and Systematics*; Futuyma, D.J., Ed.; Annual Reviews: Palo Alto, CA, USA, 2014; Volume 45, pp. 471–493.
26. Preston, D.L.; Mischler, J.A.; Townsend, A.R.; Johnson, P.T.J. Disease Ecology Meets Ecosystem Science. *Ecosystems* **2016**, *19*, 737–748. [CrossRef]
27. Smith, B.P. The potential of mites as biological control agents of mosquitoes. In *Research Needs for Development of Biological Control of Pests by Mites*; Hoy, M.A., Cunningham, G.L., Knutson, L., Eds.; University of California: Berkeley, CA, USA, 1983; pp. 79–85.
28. Rajendran, R.; Prasad, R.S. *Encentridophorus similis* (Acarina, Unionicolidae) an active predator of mosquito larvae. *Curr. Sci.* **1989**, *58*, 466–467.
29. Rajendran, R.; Prasad, R.S. A laboratory study on the life-cycle and feeding-behavior of Arrenurus madaraszi (Acari, Arrenuridae) parasitizing Anopheles mosquitos. *Ann. Trop. Med. Parasitol.* **1994**, *88*, 169–174. [CrossRef] [PubMed]
30. Hearle, E. The mosquitoes of the Lower Fraser Valley, British Columbia, and their control. *Nat. Res. Counc. Ott. Kept* **1926**, *17*, 94.
31. Bottger, K. Feeding of water mites Hydrachnellae acari. *Int. Rev. Gesamten Hydrobiol.* **1970**, *55*, 895–912. [CrossRef]
32. Laird, M. Some natural enemies of mosquitoes in the vicinity of Palmalmal, New Britain. *Trans. Roy. Soc. N. Z.* **1947**, *76*, 453–476.
33. Mullen, G.R. Acarine parasites of mosquitos 1. Critical review of all known records of mosquitos parasitized by mites. *J. Med. Entomol.* **1975**, *12*, 27–36. [CrossRef]
34. Simmons, T.W.; Hutchinson, M.L. A Critical Review of All Known Published Records for Water Mite (Acari: Hydrachnidiae) and Mosquito (Diptera: Culicidae) Parasitic Associations From 1975 to Present. *J. Med. Entomol.* **2016**, *53*, 737–752. [CrossRef]
35. Smith, I.M.; Oliver, D.R. Review of parasitic associations of larval water mites (Acari, parasitengona, Hydrachnida) with insect hosts. *Can. Entomol.* **1986**, *118*, 407–472. [CrossRef]

36. Atwa, A.A.; Bilgrami, A.L.; Al-Saggaf, A.I.M. Host-parasite interaction and impact of mite infection on mosquito population. *Rev. Bras. Entomol.* **2017**, *61*, 101–106. [CrossRef]
37. Manges, A.; Simmons, T.; Hutchinson, M. First Record of Aedes albopictus (Diptera: Culicidae) and Second Record of Aedes japonicus (Diptera: Culicidae) Parasitized by Water Mites (Acari: Hydrachnidiae) in North America. *J. Med. Entomol.* **2018**, *55*, 1617–1621. [CrossRef] [PubMed]
38. Shaalan, E.A.-S.; Bekhet, G.; Abdelmoaty, Z.; Ahmad, N.W. First Report on Mosquito Parasitic Mites in Saudi Arabia. *Pak. J. Zool.* **2016**, *48*, 1989–1992.
39. Montes-Ortiz, L.; Goldschmidt, T.; Elias-Gutierrez, M. First evidence of parasitation of a Bosmina (Cladocera) by a water mite larva in a karst sinkhole, in Quintana Roo (Yucatan Peninsula, Mexico). *Acarologia* **2019**, *59*, 111–114. [CrossRef]
40. Marshall, J.F. *The British Mosquitoes*; British Museum: London, UK, 1938.
41. Mira, G. Sulla presenza di forme larvali di un acaro acquatico parassita, della famiglia degli Hydracnidae, su alcune zanzare del genere Anopheles in A. O. I. *Boll Idrobiol Caccia E Pesca Afr. Orient. Ital* **1940**, *1*, 29–33.
42. Esen, Y.; Erman, O. A new species of the genus Arrenurus Duges, 1834 (Acari: Hydrachnidia: Arrenuridae) for the Turkish fauna: Arrenurus (Truncaturus) corsicus (E. Angelier, 1951). *Turk. J. Zool.* **2013**, *37*, 372–375. [CrossRef]
43. Leal dos Santos, F.; Thies, S.; Gonçalves, A.; Vasconcelos, K.; Ribeiro, M.; Damasceno, J.; Oliveira Dantas, E.; Leite Júnior, D. Aquatic Phoretic Mites (Acari: Hydrachnidia) Associated with Ectoparasitism of Mosquitoes (Diptera: Culicidae) in the Midwest Region of Brazil. *Adv. Entomol.* **2016**, *4*, 141–150. [CrossRef]
44. Nagel, L.; Zanuttig, M.; Forbes, M.R. Escape of parasitic water mites from dragonfly predators attacking their damselfly hosts. *Can. J. Zool.* **2011**, *89*, 213–218. [CrossRef]
45. Werblow, A.; Martin, P.; Dorge, D.; Koch, L.; Mehlhorn, H.; Melaun, C.; Klimpel, S. Hyperparasitism of mosquitoes by water mite larvae. *Parasitol. Res.* **2015**, *114*, 2757–2765. [CrossRef]
46. Kirkhoff, C.; Simmons, T.; Hutchinson, M. Adult mosquitoes parasitized by larval water mites in Pennsylvania. *J. Parasitol.* **2013**, *99*, 31–39. [CrossRef]
47. Klemm, D.J.; Lewis, P.A.; Fulk, F.; Lazorchak, J.M. *Macroinvertebrate Field and Laboratory Methods for Evaluating the Biological Integrity of Surface Waters*; Environmental Monitoring Systems Laboratory, U.S. Environmental Protection Agency: Cincinnati, OH, USA, 1990.
48. Jalil, M.; Mitchell, R. Parasitism of Mosquitos by Water Mites. *J. Med. Entomol.* **1972**, *9*, 305. [CrossRef]
49. Mullen, G. Acarine parasites of mosquitos 4. Taxonomy, life-history and behavior of Thyas barbigera and Thyasides sphagnorum (Hydrachnellae-thyasidae). *J. Med. Entomol.* **1977**, *13*, 475–485. [CrossRef] [PubMed]
50. Lanciani, C. Influence of parasitic water mites on the instantaneous death rate of their hosts. *Oecologia* **1979**, *44*, 60–62. [CrossRef] [PubMed]
51. Margolis, L.; Esch, G.; Holmes, J.; Kuris, A.; Schad, G. The use of ecological terms in parasitology (report of an ad hoc committee of the American-Society of Parasitologists). *J. Parasitol.* **1982**, *68*, 131–133. [CrossRef]
52. Mitchell, R. Major evolutionary lines in water mites. *Syst. Zool.* **1957**, *6*, 137–148. [CrossRef]
53. Lanciani, C. Sexual bias in host selection by parasitic mites of the mosquito anopheles-crucians (Diptera, Culicidae). *J. Parasitol.* **1988**, *74*, 768–773. [CrossRef]
54. Smith, B.P. Loss of larval parasitism in parasitengonine mites. *Exp. Appl. Acarol.* **1998**, *22*, 187–199. [CrossRef]
55. Bohonak, A.J.; Smith, B.P.; Thornton, M. Distributional, morphological and genetic consequences of dispersal for temporary pond water mites. *Freshw. Biol.* **2004**, *49*, 170–180. [CrossRef]
56. Martin, P.; Dabert, M.; Dabert, J. Molecular evidence for species separation in the water mite Hygrobates nigromaculatus Lebert, 1879 (Acari, Hydrachnidia): Evolutionary consequences of the loss of larval parasitism. *Aquat. Sci.* **2010**, *72*, 347–360. [CrossRef]
57. Martin, P. Specificity of attachment sites of larval water mites (Hydrachnidia, Acari) on their insect hosts (Chironomidae, Diptera)—Evidence from some stream-living species. *Exp. Appl. Acarol.* **2004**, *34*, 95–112. [CrossRef]
58. Esteva, L.; Rivas, G.; Yang, H.M. Modelling parasitism and predation of mosquitoes by water mites. *J. Math. Biol.* **2006**, *53*, 540–555. [CrossRef]
59. Kneitel, J.M.; Miller, T.E. Resource and top-predator regulation in the pitcher plant (Sarracenia purpurea) inquiline community. *Ecology* **2002**, *83*, 680–688. [CrossRef]

60. Wilke, A.B.B.; Chase, C.; Vasquez, C.; Carvajal, A.; Medina, J.; Petrie, W.D.; Beier, J.C. Urbanization creates diverse aquatic habitats for immature mosquitoes in urban areas. *Sci. Rep.* **2019**, *9*, 15335. [CrossRef] [PubMed]
61. Maimusa, A.H.; Ahmad, A.H.; Abu Kassim, N.F.; Ahmad, H.; Dieng, H.; Rahim, J. Contribution of public places in proliferation of dengue vectors in Penang Island, Malaysia. *Asian Pac. J. Trop. Biomed.* **2017**, *7*, 183–187. [CrossRef]
62. UN Intergovernmental Panel on Climate Change. Available online: http://www.ipcc.ch/report/sr15/ (accessed on 31 May 2020).