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1 **Highlights**

- 2 • Elimination of vector populations has immense potential for vector-borne disease
3 control but poses significant ecological, environmental, societal, and ethical questions
- 4 • Although vector biology has been studied primarily through the lens of vector control,
5 recent efforts have sought to understand their ecological roles in ecosystems
- 6 • While reductions in vector abundance alter biotic interactions through effects on food
7 webs, competition, and pollination, it remains unresolved whether resulting impacts on
8 biodiversity and ecosystem services is significant
- 9 • Compared to the efforts devoted to evaluating the efficacy of vector control tools, there
10 are few environmental impact assessments
- 11 • Evaluating the ecological significance of vectors requires quantitative, long-term
12 monitoring bringing together ecologists, botanists, entomologists, molecular biologists,
13 and data scientists.

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1 **The ecological significance of arthropod vectors of plant, animal, and human pathogens**

2

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15

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17

18 **Abstract**

19 Vector control is a cornerstone in the fight against vector-borne pathogens. However, the impact
20 on ecosystem functioning of reducing or eliminating arthropod vector populations remains
21 poorly understood. Vectors are members of complex ecological communities, and recent
22 studies suggest that population suppression may alter food web dynamics (bottom-up and top-
23 down trophic cascades), inter- and intraspecific competition, and plant pollination. Other
24 possible overlooked roles are also proposed. With examples from vectors of plant, animal, and
25 human pathogens, we highlight that although the ecological roles of most vector species may
26 be redundant with other non-vector species, changes in vector abundance alter biotic
27 interactions and are thus unlikely to be neutral on ecosystem functioning.

28

29 The ecological roles of arthropod vectors: the hidden side of their 30 biology

31 Arthropod vectors are detrimental to human well-being as they can transmit human, plant, and
32 livestock pathogens. Vector-borne pathogens are responsible for ~ 700,000 human deaths
33 annually [1], and infections in domesticated plants and animals cause significant economic
34 losses [2]. Arthropod vectors of human and animal pathogens include ticks, fleas, triatomine
35 bugs, and several dipteran species (mosquitoes, blackflies, sandflies, tsetse flies, biting midges)
36 (**Box 1**). Together they can transmit numerous pathogens (viruses, bacteria, protozoa, and
37 nematodes), causing diseases as diverse as Dengue, West Nile fever, Zika, Malaria, African
38 swine fever, heartwater disease, bluetongue, African trypanosomiasis, leishmaniasis, Chagas
39 disease, Lyme disease, lymphatic filariasis, onchocerciasis, and plague. Most plant pathogen
40 vectors belong to the order Hemiptera. Aphids, whiteflies, thrips, leafhoppers, and planthoppers
41 are the major vectors of plant viruses, while jumping plant-lice, leafhoppers, planthoppers, and
42 spittlebugs transmit bacteria [3]. These pathogens are responsible for a wide range of plant
43 diseases, including cereal yellow dwarf, cassava mosaic virus, rice yellow mottle virus,
44 Huanglongbing of citrus, Pierce's disease and Flavescence dorée of grapevines. The
45 Heteroptera are the only group of insects that transmit pathogens infecting both humans (i.e.,
46 Chagas disease caused by the protozoan parasite *Trypanosoma cruzi* and transmitted by
47 triatomine bugs) and crops (e.g., the trypanosomatid *Herpetomonas* spp. transmitted by
48 *Leptoglossus zonatus*).

49 When control measures that directly target pathogens (vaccines, drugs) are unavailable or
50 inefficient, vector population management is the most effective means of disease prevention
51 (**Box 2**). Although vector control has long relied on insecticides, awareness of their impact on
52 our health and the environment and the spread of insecticide resistance have led to the search
53 for new control tools. Among novel interventions, a promising development is the release of
54 genetically-modified sterile transgenic arthropods. For example, in the fight against malaria, it
55 is now possible to use CRISPR-based gene-drive technology to spread a mutation that blocks
56 female reproduction. A recent study has demonstrated the effectiveness of this technique in
57 suppressing mosquito populations housed in large indoor cages [4]. While this new technology
58 offers bright prospects for effective control of arthropod vector populations, several logistical
59 and ethical issues must be resolved before this strategy can be effectively deployed in the field.
60 Of particular concern are the possible adverse ecological consequences of reducing or even
61 eliminating vector populations.

62 Here, we critically assess the diversity of **ecological roles (see Glossary)** played by
63 arthropod vectors. Vectors are, of course, best-known for their role in indirectly regulating the
64 population dynamics of humans, animals, and plants through the transmission of virulent
65 pathogens [5]. However, recent examples from diverse arthropod vectors suggest direct
66 influences on food webs (bottom-up and top-down trophic effects), inter and intraspecific
67 competition, and pollination. As such, the suppression of arthropod vectors is likely to have
68 important consequences on **ecosystem functioning, stability, and biodiversity (Figure 1)**. In
69 bringing together thinking about human, animal, and plant-pathogen vectors, we emphasize the
70 importance of a **One-Health perspective** [6].

71

72 **Food web links**

73 Food webs represent the feeding links among species in an ecosystem (who eats whom) and the
74 relative amount of energy flowing along the different trophic links (strength of the interactions).
75 Apart from host-parasite interactions, energy flows upwards from many small organisms at the
76 web's base into larger, rarer organisms at the top of the web. Typically, arthropods are both
77 predators and prey and thus occupy a central position in food webs. Such central **nodes** are
78 critical as changes in abundance may precipitate both bottom-up and top-down trophic
79 cascades. In a rainforest ecosystem, for example, reduction in arthropod abundance -
80 presumably because of climate change – has driven declines in insectivores, including lizards,
81 frogs, and birds [7]. Evidence for trophic cascades and food-web collapse following the
82 implementation of vector control is currently limited. Identifying such effects requires
83 knowledge of the interactions between the focal organism and other species present in the
84 community.

85

86 *Bottom-up effects*

87 Arthropod-vector control, and collateral reductions in non-target species, may impact predators
88 that rely on these species for food. A recent dietary analysis of arthropod species present in the
89 faeces of western bluebirds in California vineyards revealed that *Aedes* spp. was by far the most
90 common item recovered, occurring in 51.2 and 49.1% of samples from adult and nestling,
91 respectively [8]. Furthermore, studies are beginning to examine the effects of vector control on
92 the food webs in which they reside. For example, long-term field monitoring and mesocosm
93 experiments following mosquito control with the larvicide *Bacillus thuringiensis* var.
94 *israelensis* (Bti) have revealed largely negative consequences of the Bti-induced reduction in

95 mosquito density (along with reductions in non-target chironomids). These effects include
96 reductions in the abundance, size, or diversity of aquatic and terrestrial predators, including
97 dragonflies and damselflies [9], newts [10], frogs [11], and birds [12]. Therefore, reductions in
98 mosquito density or non-target species may affect predators and have cascading effects on other
99 trophic links (**Figure 2**).

100 In contrast to the above examples, a short-term field study in Kenya revealed that a
101 single application of long-lasting microbial larvicides significantly reduced the density of the
102 two major malaria vectors *Anopheles gambiae s.l.* and *An. funestus s.l.*, with no measurable
103 direct or indirect effects on the abundance and diversity of eleven taxa, including fishes, frogs,
104 snails, and aquatic insects [13]. Likewise, Hanowski et al. [14] found no evidence that red-
105 winged blackbird reproduction, growth, or foraging behavior were affected by mosquito
106 suppression following Bti treatment in the USA.

107 The consequences of the complete eradication of *Anopheles* malaria vectors, as
108 proposed by applying gene drive-modified mosquitoes, remains controversial. On the one hand,
109 because mosquito larvae and adults, including *Anopheles*, account for an important portion of
110 the biomass in a wide range of wetland ecosystems and represent resources for multiple aquatic
111 and terrestrial predators (fishes, bats, birds, salamanders, spiders, arthropods) [15,16], some
112 authors suggest that mosquito suppression could reduce predator population sizes. This could
113 then be amplified by a series of secondary cascade effects with ultimate ecosystem disruption
114 [17,18]. On the other hand, based on their comprehensive literature survey, Collins et al. [19]
115 argued that most *Anopheles* predators are **generalists**. As such, trophic links between *Anopheles*
116 with their predators may be weak, and their removal may only trivially impact ecosystem
117 functioning [19]. However, a note of caution is warranted because recent research suggests that
118 eliminating a weak node in a food web can still precipitate **network** collapse and biodiversity
119 loss [20].

120 Similar considerations may apply to other Dipteran-vector species. While the predators
121 of sandflies, midges, black flies, and tsetse flies are less well known than that of mosquitoes, a
122 diversity of aquatic and terrestrial predators, including hydra, moths, spiders, ants, crickets,
123 odonatan, other Diptera, fish, and birds, feed on the larvae and adults of these vectors [21–24].
124 The predation is likely density-dependent with substantial spatial and temporal variation in the
125 contribution of these vectors to the diet of their predators. At very high densities, these insects
126 could even be prime candidates for human entomophagy, as has already been observed in
127 Thailand [25]. Dejections of arthropod larvae in their aquatic habitats can also be an essential

128 resource for many microorganisms and contribute to soil fertilization. For example, blackfly
129 dejections drifting in Sweden streams and rivers can reach 429 tons per day, or as many as 6000
130 elephants defecating each day [25].

131 Tick predators include ants, beetles, and many bird species and are also believed to be
132 generalists whose populations do not entirely depend on ticks as prey [26]. However, oxpeckers
133 provide an exception to this rule as their diet is almost exclusively composed of ticks [27].
134 Indeed, tick control using the widespread application of acaricides to livestock has contributed
135 to population declines in both species of oxpeckers in South Africa [27].

136 While most predators of animal and human pathogen-vectors seem to be generalists,
137 predator-vector or parasitoid-vector relationships within plant systems tend to be more specific.
138 The well-known plant-aphid-ladybug interaction is illustrative, where reduction in aphid
139 biomass can have significant bottom-up effects on predatory ladybugs, not only at a field scale
140 but also at the landscape level [28]. Likewise, leafhoppers, including several key vector species
141 like *Macrostelus quadrilineatus* and *Graminella nigrifrons*, can represent a significant part of
142 the endangered lesser prairie chickens' diet. Elimination of these abundant vector species,
143 which are indicators of grassland habitat health, may have unintended consequences on their
144 predators and destabilize the food web dynamic [29]. The aforementioned DNA metabarcoding
145 analysis in California vineyards found that a significant proportion of the western bluebird diet
146 was composed of Hemipteran vectors of plant pathogens, including *Aphis craccivora*, a vector
147 of numerous plant viruses and the leafhopper *Graphocephala atropunctata* (formerly *Hordnia*
148 *circellata*), the most important vector of *X. fastidiosa* that causes Pierce's disease to grapevines
149 in coastal California [8].

150 Hemipteran populations can be regulated by parasitic wasps (i.e., parasitoids), which
151 often have a narrow host species range. Eliminating or reducing hemipteran vectors may limit
152 the long-term maintenance of parasitoid populations, resulting in biodiversity loss. For
153 example, the abundance of the *Anagrus* spp. parasitoids decreased when the density of
154 *Erythroneura* spp. leafhopper-hosts, a serious pest to grapes in North America and a suspected
155 vector of viruses and phytoplasma, decreased [30] (see also [31,32] for similar examples of
156 specialist parasitoids of tsetse flies and ticks). However, in some cases, a decrease in target
157 vector density can be compensated by host switches to related non-vector host species. For
158 example, in La Reunion island, the successful eradication of the introduced psyllid vector
159 *Diaphorina citri* by a released parasitoid was facilitated by the presence of a native psyllid that
160 served as an alternative host for the parasitoids when the vector populations declined [33]. Diniz

161 et al. [34] showed that the release of parasitoids in areas bordering commercial citrus groves
162 (e.g., abandoned or organic groves, residential trees, etc.) had the potential to maximize actions
163 for *D. citri* control.

164 Hemipterans can also have important bottom-up trophic effects through their production
165 of honeydew. In a two-year field trial in New Zealand, the deposition of honeydew under the
166 plant canopy by the giant willow aphid *Tuberolachnus salignus* increased microbial biomass
167 and the abundance of yeast and mesofauna in the underlying soil [35]. Furthermore, adult
168 parasitoids of hemipteran vectors readily feed on honeydew excreted by aphids, whiteflies,
169 mealybugs, and psyllids (e.g.[36]). Therefore, the control of these vector populations could
170 result in the loss of their parasitoids and cascading effects on higher trophic levels, such as on
171 the hyperparasitoid communities [37]. Mosquito vectors also benefit from consuming
172 carbohydrates from honeydew [38]. Thus, within a One-Health context, controlling aphid
173 vectors could have the additional benefit of reducing mosquito access to sugar meals and
174 possibly limiting the transmission of mosquito-borne pathogens.

175 *Top-down effects*

176 Variation in vector density can also affect lower trophic levels. The larvae of most vectors of
177 human and animal pathogens feed on primary producer microorganisms (bacteria, protozoans,
178 rotifers, diatoms and algae) and organic waste in either aquatic (mosquitoes, blackflies) or
179 humid terrestrial (midges, sandflies) environments [39]. Arthropod vectors may structure the
180 community of these microorganisms and influence processes such as the decomposition of
181 organic detritus and water purification in complex ways [40]. For example, a reduction in
182 mosquito density can increase natural protozoan richness and abundance in Swedish wetlands
183 [41], or alter the bacterial community in experimental microcosms [42]. Other larval stages of
184 dipteran vectors (Simuliidae, Phlebotominae, Ceratopogonidae) may play comparable roles in
185 ecosystems [25], although their ecological roles can sometimes be more specific. For example,
186 silk production by blackfly larvae helps retain organic matter for microorganisms and provides
187 habitat for other macroinvertebrates [43].

188 Arguably the most important top-down trophic effect of vectors is the regulation of the
189 population dynamics of their vertebrate and plant hosts and the resulting impact of
190 hematophagy and phytophagy, respectively (irrespective of pathogen transmission). Effects on
191 host morbidity and mortality and changes in host behaviour in response to pervasive vector
192 feeding can alter food web dynamics and cascade through the entire ecosystem. For example,
193 heavy tick and flea infestations, as well as black fly outbreaks, are particularly associated with
194 these direct detrimental effects on host populations [43–46]. However, this may not always be

195 the case [47]. Under natural conditions, control of these hematophagous vectors could lead to
196 host population growth with consequences on other trophic levels (e.g., increased prey
197 abundance for carnivorous predators). As one example of a behavior-mediated trophic cascade,
198 a study in North America found that herbivorous mammal hosts can perceive the risk of tick
199 infestation and avoid grazing in areas with a high density of the tick *Amblyomma americanum*
200 [48], thus possibly generating spatial variability in primary production (i.e. decreased level of
201 herbivory pressure in tick-abundant areas).

202 Many hemipteran vectors cause direct damage to their host plants and thereby
203 drastically regulate their population growth [49–52]. Likewise, hemipteran control can improve
204 plant health and benefit the surrounding agrosystem. For example, **agroecological approaches**
205 to reducing pest populations without completely eradicating them can sustain natural enemies
206 (e.g. ladybugs and generalist parasitoids), useful for other surrounding crops [53]. A healthy
207 host-plant population can also provide resources (e.g. nectar, pollen) to other community
208 members, including natural enemies of the vectors, and help improve biological control at large
209 scales [54].

210 Reducing vector population size inevitably decreases population genetic variation,
211 which can have top-down effects on microbial community members. Hemipterans often rely on
212 bacterial symbionts to synthesise essential amino acids [55] or aid in protection from enemies
213 [56]. Chong and Moran [57] showed that genetic variation in the pea aphid *Acyrtosiphon*
214 *pisum* could affect the regulation of their obligate heritable symbiont *Buchnera aphidicola*. In
215 addition to vertical transmission, horizontal transmission of bacterial symbionts to the same or
216 different species can occur during feeding on plants [58] and could directly impact other trophic
217 levels. Oliver et al. [59] showed that aphid infection with the bacterial symbiont *Hamiltonella*
218 *defensa* increased in frequency in the presence of parasitoid wasps. It can therefore be expected
219 that reductions of hemipteran populations could result in the degradation of the networks of
220 species interactions with cascading effects on ecosystem functioning. Vectors of human and
221 animal pathogens also harbour a large community of naturally occurring entomopathogens
222 and/or symbionts (viruses, bacteria, protists, fungi) [60]. The **microbiome** of hematophagous
223 vectors also plays critical roles in interactions with the vertebrate hosts, as well as in the
224 transmission of pathogens [60]. The extent of the ecological roles conferred by the microbiome
225 is only beginning to be revealed, and gaps remain in the understanding of the microbiome-
226 mediated consequences of vector suppression on ecosystem functioning [61].

227

228 **Inter- and intra-specific competition**

229 Resources at breeding sites of dipteran vectors are generally limiting, and intraspecific resource
230 competition can drive population dynamics. For example, a recent study on the arctic mosquito
231 *Aedes nigripes* showed strong negative feedback between larval abundance and per capita
232 survival but no link between vector mortality and predator density, suggesting that intraspecific
233 competition can be more important than predators [62]. Similarly, predator-induced mortality
234 appeared to increase population survival in *Ae. aegypti*, a counter-intuitive result apparently
235 explained by the reduction in intraspecific competition generated by predation [63]. Although
236 the outcome of such interactions may depend on the local context (diversity and abundance of
237 predators, resource quality and quantity, permanent vs temporary breeding sites, and other
238 seasonal and environmental fluctuations, [64]), it is possible that imperfect larval control could
239 have the unintended effect of increasing adult emergence and pathogen transmission when
240 populations are released from intraspecific competition.

241 Because host plants are generally very abundant in agrosystems, intraspecific
242 competition among hemipteran vectors is often assumed to be weak. However, intraspecific
243 competition is common in these systems and is generally mediated by host plant defenses (e.g.
244 intraspecific variability in susceptibility of the insects to plant defenses) [65]. For example, in
245 the planthopper *Nilaparvata lugens*, a major pest and virus vector to rice, intraspecific
246 competition caused higher vector mortality on a rice variety with high levels of anti-herbivore
247 defenses than on the variety with low defense levels [65].

248 Arthropod vectors may also compete with other species. At the larval stage, mosquitoes
249 compete with aquatic micro and macrofauna. In a laboratory microcosm experiment, ciliates
250 and rotifers, which are usually considered prey for mosquito larvae, reduced the population
251 growth of *Culex nigripalpus* through competition for resources such as flagellates and bacteria
252 [66]. In another experiment, population growth rates of non-predatory tadpoles and mosquitoes
253 (*Limnodynastes peronei*-*Culex quinquefasciatus*, and *Crinia signifera*-*Ochlerotatus australis*)
254 were reduced when housed together, suggestive of resource competition [67].

255 Interspecific competition can play key roles in the population dynamics of plant-
256 pathogen vectors. Such competition can have important implications for vector management.
257 For example, the cultivation of transgenic Bt cotton has favored the tarnished plant bug *Lygus*
258 *hesperus*, a key agricultural pest in the western United States and the vector of *Pantoea ananatis*
259 and *Serratia marcescens*, over its more Bt-susceptible Lepidopteran competitors [68]. A recent
260 study found that interspecific competition can even be mediated by the pathogen being

261 transmitted [69]. For example, the barley yellow dwarf virus can enhance the thermal tolerance
262 of its vector, the aphid *Rhopalosiphum padi*, allowing it to expand its ecological niche to
263 warmer regions and escape competition from another aphid, *R. maidis*, which is native to colder
264 regions [69]. Interspecific competition between two vector species can sometimes affect higher
265 trophic level. In a recent study, the presence of the thrip vector *Frankliniella occidentalis*
266 directly reduced the performance of its competitor, the aphid vector *Myzus persicae*, but the
267 thrip's aggregation hormone repelled an aphidophagous hoverfly [70].

268 Invasive arthropod vectors offer a unique opportunity to study inter-specific
269 competition. Competition involving invasive *Ae. albopictus* and *Ae. aegypti* in North America
270 has been well documented [71]. *Aedes albopictus* tends to be a superior larval competitor,
271 resulting in either species displacement or reduction of the relative abundance of *Ae. aegypti*
272 [72]. A similar pattern of species displacement by a superior competitor is seen with the
273 invasive Asian blue tick *Rhipicephalus microplus*, the main vector of *Babesia bovis*, which is
274 currently displacing many indigenous *Rhipicephalus* species in tropical regions [73]. The
275 whitefly *Bemisia tabaci* species complex is an emblematic example of highly invasive species
276 able to adapt to new environments and replace closely related non-invasive species [74,75].
277 These species replacements have often been accompanied by serious outbreaks and/or
278 epidemics [76,77], likely leading to major disruptions of equilibrium in multitrophic chains.

279 Although interspecific competition has long been described as a powerful force shaping
280 local ecosystem functioning and structuring communities [78], the ecological consequences of
281 interspecific competition involving arthropod vectors remain poorly understood. Furthermore,
282 competition can result in changes in vector behavior and physiology, with cascading effects on
283 population and community ecology and eventually pathogen transmission [79].

284

285 **Pollination**

286 The vast majority of angiosperms rely on arthropods for pollination. In addition to bees, many
287 flies are important plant pollinators, including of crops [80]. Thus, dipteran vectors may be
288 providers of this valuable ecosystem service. Mosquitoes, blackflies, sandflies, and biting
289 midges frequently visit flowers to harvest nectar for energy, although it is unknown if these
290 visits facilitate pollination. Most information on the contribution of vectors to pollination has
291 been anecdotal, an exception being the ceratopogonids, whose key role as pollinators of the
292 cacao tree is relatively well described [81]. However, most ceratopogonid pollinators belong to
293 the genus *Forcipomyia*, which is not considered a pathogen vector (but see [82]). The

294 ceratopogonid vectors in the genus *Culicoides* are generally considered poor pollinators.
295 However, *C. parensis*, a vector of the Oropouche virus, and *C. insignis*, a vector of Bluetongue
296 virus, can pollinate hevea and cacao trees, respectively [83]. Maintaining diverse and abundant
297 larval breeding sites for pollinating midges in cacao fields has been proposed as a strategy for
298 increasing cacao yields. However, these breeding sites can be shared with larvae of *Anopheles*,
299 *Culex*, and *Aedes* vectors [84] and may have the unintended consequence of increasing
300 pathogen transmission. Thus, the removal or creation of these breeding sites must be considered
301 within a one-health perspective.

302 While the importance of mosquitoes to global pollination is unclear, several
303 observations suggest that it may be more common than previously thought [85,86]. For
304 example, population cage experiments with tansy flowers found that *Cx. pipiens* effectively
305 transferred pollen between inflorescences, resulting in seed-set [87]. Similar experiments with
306 other dipteran vectors such as sandflies or blackflies could provide interesting new perspectives
307 on the significance of arthropod vectors as pollinators. Furthermore, quantifying the relative
308 pollination efficacy of dipteran vectors such as mosquitoes and other well-known fly pollinators
309 such as Syrphidae or Calliphoridae will elucidate how much plants rely on dipteran vectors for
310 their reproduction.

311 Among vectors of plant pathogens, thrips act as pollinators of plants as diverse as
312 cycads, elders, eggplants, bearberry, orchids, *Shorea spp.*, *Hopea spp.*, and *Macaranga spp.*
313 [88]. Aphids, along with thrips, could also contribute to the pollination of the cinquefoil
314 *Potentilla rivalis* and the celery-leaved buttercup *Ranunculus sceleratus* [89]. Phytophagous
315 vectors could also have an indirect role in pollination because they attract and maintain
316 predatory pollinators. Hoverflies (Syrphidae), for instance, are both predators of aphids and
317 other hemipteran vectors at the larval stage and important pollinators as adults [90].
318 Coccinellidae, the most famous aphid eater, along with parasitoids flies and wasps, are also
319 increasingly suspected of contributing to crop pollination systems [80,90]. The suppression of
320 hemipteran vectors could therefore have antagonistic effects on crop yields.

321

322 **Other ecological roles**

323 The mere presence and abundance of a vector species in a habitat can protect it from human
324 activities, thereby limiting some of the key drivers of global biodiversity loss. For example,
325 tsetse flies and trypanosomiasis prevent the expansion of livestock farming to wild areas and

326 prevent conflicts between humans and lions [91]. Likewise, the nuisance of mosquitoes, midges
327 and blackflies curtail human activities in regions where they reach high densities.

328 In disease-endemic areas, humans and animals receive many more bites from uninfected
329 vectors than from infected individuals. Recent studies have shown that salivary proteins
330 delivered by uninfected vectors can be immunogenic and confer protection to subsequent
331 pathogen exposure [92]. There has even been a clinical trial of a vaccine targeting mosquito
332 saliva proteins in hopes of finding a universal vaccine providing protection to mosquito-borne
333 pathogens [93]. Further research is needed to assess how common “vaccination services” are
334 among hematophagous vectors and explore whether similar effects occur in plants.

335

336 **Concluding Remarks**

337 While vector-borne pathogens of humans, animals, and plants continue to impact
338 humankind negatively, the ecological significance of arthropod vectors is only beginning to be
339 uncovered with multiple functions fulfilled, such as food web links, pollination and competitive
340 interactions. The use of control tools, including novel technologies that suppress, reduce, or
341 entirely eliminate vector populations, has immense potential but poses significant ecological,
342 environmental, societal, and ethical questions [94] (**see Outstanding Questions**). More studies
343 need to address how changes in vector species abundance affect ecosystem integrity and
344 potentially lead to detrimental consequences on biodiversity. Untangling the influence of such
345 changes on ecological network stability and persistence is complex and requires integrated
346 longitudinal investigation within and among interaction levels in both aquatic and terrestrial
347 ecosystems. Collaborative research bringing together ecologists, botanists, entomologists, and
348 data scientists is needed to gather comprehensive data and then apply novel methodologies such
349 as network analysis [95] to predict how a reduction in vector populations will affect ecosystem
350 processes and stability. For example, DNA metabarcoding analyses of the gut contents of
351 vectors and their predators can offer unique opportunities to gather large-scale, long-term
352 network data sets [96]. Another research avenue would be to examine how the infection status
353 of vertebrate and plant hosts or the infection of the vector itself can cause changes in biotic
354 interactions and lead to changes in ecosystem functioning [97].

355 Vectors will likely exhibit weak links with other organisms in the network of
356 interactions in their ecological community: they are neither the only resource for their predators
357 nor the only consumer of their prey. Similar **functional redundancy** may characterize the role
358 of vectors as pollinators. As such, if the ecological roles of vectors within an ecosystem are

359 redundant with non-vector species, then there may be a legitimate ecological argument
360 supporting their suppression or elimination. However, research suggests that even the
361 elimination of weak nodes in an ecological network may result in collapse and biodiversity loss
362 [20]. Species interactions are so complex when considering weight coefficients of the
363 interactions that it becomes difficult to predict the consequences of removing a node on
364 ecosystem functioning [98]. In addition, two species can be redundant on well-known traits
365 (e.g. diet, mobility) but differ in other traits (e.g. difference in phenology or micro spatial habitat
366 use) with consequences on interacting species (predators, competitors, prey). Suppression or
367 elimination of a vector species does not guarantee a similar compensatory gain in the biomass
368 of the presumably functionally equivalent species because specific rate-limiting growth factors
369 such as temperature, may be different.

370 We focused on the possible adverse effects of reduced vector abundance (in response to
371 vector control) on ecological processes. There is very little research on the potential benefits of
372 increasing the abundance of an introduced vector species. In addition to the adverse ecological
373 effect of declining vector abundance, vector control measures such as insecticides may impact
374 ecosystem functioning by directly harming non-target species; this is well illustrated in studies
375 of tsetse flies and ticks, where effects on non-target species of insecticide-impregnated
376 traps/targets and “pour-on” for cattle (a mixture of repellents and insecticides) destabilize food
377 webs with cascading adverse effects on biodiversity [99]. Similarly, for agriculture, the
378 resurgence of pest outbreaks or epidemics can often be associated with a breakdown in
379 multitrophic relationships due to the unintended effects of insecticides on non-target organisms
380 [100].

381 Without the extensive time-series investigations needed to quantify how much ecosystem
382 functioning and stability rely on vector species, it remains difficult, if not impossible, to
383 accurately predict the consequences of the removal or reduction of vector populations. If their
384 ecological importance proves significant, then perhaps disease control methods targeting
385 pathogens (drugs, vaccines, transmission-blocking strategies) should be encouraged in lieu of
386 vector-eradication efforts. Likewise, when considering new technologies such as genetically
387 modified vectors, introducing pathogen-resistant vector lineages (i.e., population replacement)
388 might be less harmful to ecosystem functioning than sterile lines (i.e., population suppression).
389 Presently, new vector control technologies are advancing much faster than research on their
390 potential risks. Research on the control of vector-borne diseases needs to consider how people
391 perceive the vector, the disease, and their management (**Box 3**). These concerns should not be

392 ignored. All stakeholders should be involved in discussions of the consequences of vector
393 elimination, a debate that needs to be better informed on the unexpected ecological
394 consequences of such efforts.

395

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400

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653 Glossary

654 **Agroecological approaches.** Control methods derived from agroecology, i.e., the study of
655 agricultural systems from an ecological perspective that integrates biological, social, and
656 economic dimensions. These methods design and/or manage agricultural systems using
657 ecological principles.

658 **Ecological roles:** Any characteristic of the biology of an organism (individual, population,
659 species) that has repercussions on ecosystem processes. Here, this is the contribution, role,
660 process, or function that an individual, population, or species plays in its community or
661 ecosystem (decomposer, consumer, resource, pollinator, competitor, etc.).

662 **Ecosystem functioning:** the set of ecological processes that operate within the ecosystem and
663 are performed by organisms fulfilling specific ecological roles (e.g. decomposition, nutrient
664 and water cycling, pollination, competition, etc.).

665 **Ecosystem stability:** the ability of the ecosystem to maintain its ecological processes and
666 structure in the face of disturbance (in this case, the suppression of arthropod vectors).

667 **Biodiversity:** Biodiversity is a multidimensional concept, encompassing (i) species diversity,
668 (ii) functional diversity (the diversity of ecological roles), (iii) phylogenetic diversity (the
669 phylogenetic distance among species), and (iv) genetic diversity among and within species.

670 **Functional redundancy:** When more than one species more or less performs the same
671 ecological role (decomposer, consumer, resource, pollinator, etc.) within a community or
672 ecosystem. Because different species play similar ecological roles, this concept often assumes
673 that a redundant species can be lost with minimal impact on ecosystem processes.

674 **One-Health perspective:** a holistic, transdisciplinary, and multisectoral approach, based on the
675 idea that humans do not exist in isolation but that their health is also closely linked to that of
676 other living organisms (animals or plants) in their ecosystem.

677 **Nodes:** The components of a network. In this case, nodes represent organisms (species,
678 populations, or individuals) in a community involved in biotic interactions (predators, prey,
679 pollinators, competitors, etc.).

680 **Network:** the topology of nodes (representing individuals, populations or most often species in
681 communities) and the strength of the links between them (biotic interactions). Organisms
682 (species, populations, individuals) in communities are connected through networks of biotic
683 interactions. The network can represent ecosystem functioning and stability and displays
684 characteristics such as connectance (the proportion of realized out of all possible links), or
685 modularity (the degree to which organisms form distinct clusters of tightly interacting nodes).

686 **Generalist:** A predator that can feed on a large range of prey. In contrast, specialist predators
687 feed on a single or narrow range of prey species. Since generalists are not tied to a single prey
688 species, their populations can be maintained even in the absence of a given prey species (in this
689 case, the suppression of a vector species).

690 **Microbiome:** The set of symbiotic and/or pathogenic microorganisms (bacteria, fungi, protists,
691 viruses) associated and living in an arthropod individual, population or species.

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695 **Box 1. Overview of the diversity of arthropod vectors of human, animal, and plant** 696 **pathogens.**

697 Important dipteran vectors of human and animal pathogens (**Figure I**) include *Culex pipiens*
698 (a), which transmits arboviruses and lymphatic filariasis (LF); *Aedes albopictus* (b), which
699 transmits Dengue, Chikungunya, Zika, and Yellow fever viruses, and LF; and *Anopheles*
700 *gambiae* (c), which transmits *Plasmodium* parasites, LF and viruses. Other dipteran vectors
701 include sandflies such as *Phlebotomus perniciosus* (d), which transmit *Leishmania*; the black
702 flies *Simulium spp.* (e), which transmit onchocerciasis; the biting midges such as *Culicoides*

703 *nubeculosis* (f), which transmit the Bluetongue virus; and the tsetse such as *Glossina palpalis*
704 *gambiensis* (g), a vector of human and animal African trypanosomes. Triatomine such as
705 *Triatoma sanguisuga* (h) are vectors of *Trypanosoma cruzi*. The Siphonaptera (fleas) such as
706 *Pulex irritans* (i) are vectors of the bacterium *Yersinia pestis*. Ticks such as *Ixodes scapularis*
707 (j) can transmit bacteria *Anaplasma* or *Borrelia* causing Lyme disease, Babesia, and viruses
708 causing African swine fever or Crimean-Congo hemorrhagic fever. The majority of vectors of
709 plant pathogens are hemipterans, including psyllids such as *Cacopsylla pruni* (k), vector of
710 phytoplasma; whiteflies such as *Bemisia tabaci* (l), which transmit geminiviruses; aphids such
711 as *Acyrtosiphon pisum* (m), vector of pea enation mosaic virus; mealybugs such as
712 *Planococcus ficus* (n), which transmit grapevine leafroll ampelo viruses; leafhoppers such as
713 *Homalodisca vitripennis* (o), vectors of *Xylella fastidiosa*; planthoppers such as *Nilaparvata*
714 *lugens* (p), which transmit two viruses, rice ragged stunt virus and rice grassy stunt virus; and
715 spittlebugs such as *Philaenus spumarius* (q) which can transmit *Xylella fastidiosa* in Europe.
716 Three other taxa also play significant roles in the transmission of pathogens to plants: the
717 heteropterans such as *Leptoglossus zonatus* (r), transmitting the trypanosomatid
718 *Herpetomonas* infecting corn; thrips such as *Frankliniella occidentalis* (s), which transmit
719 tospoviruses; and chrysomelids such as *Cerotoma trifurcata* (t), known to transmit bean pod
720 mottle virus to beans. Each panel is named after the minimum taxonomic unit (super-family,
721 family, sub-family, or genus), within which arthropod vectors can be found. For example,
722 panel (g) is named after the genus *Glossina* because African Trypanosomes are transmitted by
723 several species belonging to this genus. In contrast, panel (i) is named after the subfamily
724 Triatominae because *Trypanosoma cruzi* can be transmitted by different genera (*Rhodnius*,
725 *Triatoma*, or *Panstrongylus*) in this sub-family. Likewise, panel (k) is named after the super-
726 family Psylloidea because vectors can be found in two families (Psyllidae, Triozidae).

727

728 **Figure I in Box 1.** Four major groups of hematophagous arthropods are vectors of human and
729 animal pathogens (blue panels), namely dipterans ((a)-(g)), Triatominae (h), Siphonaptera (i),
730 and Ixodoidea (j). Vectors of plant pathogens (green panels) comprise three orders of
731 phytophagous insects, namely Hemiptera (panels (k)-(r)), Thysanoptera (s), and Coleoptera
732 (t). Photo credits: (a) (c) (d) (g) Nil Rahola, MIVEGEC/IRD; (b) (l) (q) Jean-Yves Rasplus,
733 INRAE; (e) Christian Arghius, Flickr; (f) JB Ferré /EID-Méd; (h) Matthew Bertone, NC State
734 University; (i) Walter P. Pfliegler, Univ Debrecen, Flickr; (j) (t) Gilles Arbour, Répertoire des
735 Insectes du Québec, Flickr; (k) Nicolas Sauvion, INRAE; (m) Nicolas Sauvion & Bruno

736 Serrate, INRAE; (n) Kent Daane, Univ. California, Berkeley; (o) Rodrigo Krugner USDA-
737 ARS; (p) Stanley Tang, Flickr; (r) W.O. Ree; (s) Matthew Bertone, NC State University.

738

739 **Box 2. A brief overview of the diversity of vector control tools**

740 Vector control aims to prevent or reduce the intensity of transmission of vector-borne
741 pathogens to limit crop losses or to limit human or animal disease outbreaks. In most cases,
742 targeting vectors is the only means of controlling vector-borne diseases because no effective
743 vaccines or treatments are available. Many control methods have been developed against
744 several vector species or specific to one species.

745 Mechanical/physical control includes all methods to prevent contact between the vector and
746 its host directly or indirectly by reducing vector density. The approaches used can be
747 eliminating breeding sites, infrastructure and landscape (draining swamp, wetlands, and
748 barrier plants) management, personal protection (nets), and modification of cropping
749 practices.

750 Chemical control relies on synthetic neurotoxic insecticides that kill the arthropod vectors
751 immediately after exposure. Despite being a fast solution, the benefits of chemical control are
752 hampered by the evolution of resistance. Also, the toxicity of these products for humans, non-
753 target organisms, and the environment has led to more safety regulations that dissuade
754 industries from developing new compounds. Biopesticides are molecules derived from
755 microorganisms, but despite their biological origin and selectivity, their production and
756 massive use resemble synthetic insecticides. They can be toxic molecules used to reduce
757 population density, such as bacterial toxins (Bti, Bs) or analogues of biological molecules
758 used to disturb vector life cycles (pheromones, growth regulators, reproductive hormones).

759 Biological control of vectors aims to sustainably control or reduce vector populations below
760 an acceptable epidemic risk threshold while avoiding deleterious effects on ecosystems. The
761 most common tools are living organisms such as predators and parasitoids that reduce vector
762 populations in a density-dependent manner. In addition, microorganisms such as fungi,
763 viruses, and bacteria can kill insects (entomopathogenic fungus, densovirus) or reduce
764 population density by acting as sterilizing symbionts.

765 Genetic control includes methods of vector genome modification and the release of large
766 numbers of males, either to sterilize and suppress vector populations or to replace natural
767 populations by pathogen-resistant vectors. Irradiation-induced DNA damage renders males

768 sterile, which can reduce reproductive output when females mate with these males. CRISPR
769 technology allows for precise genome modifications of vectors (transgenesis) or important
770 vector symbionts (paratransgenesis). CRISPR technology also facilitates gene-drive systems
771 that promote the rapid spread of the introduced mutations through the population. Breeding
772 approaches are also a form of genetic control and consist of selecting plant genotypes that are
773 resistant to the pathogen or the vector.

774 **Figure I in Box 2.**

775 **Schematic representation of the various methods used to control arthropod vectors of**
776 **human, animal, and plant pathogens**

777

778 **Box 3. The social perception of arthropod vectors and their control.**

779 **Perceptions of arthropods**

780 Some arthropods are viewed positively for their aesthetic value (e.g., butterflies and
781 dragonflies), as symbols of good luck (e.g., ladybugs), and others for their usefulness as
782 pollinators (e.g., honeybees) or protein source (e.g., migratory locusts). However, in general,
783 they are perceived as nuisances and even as existential threats. Therefore, it would not be
784 surprising if people were more willing to eliminate them than to preserve them.

785 **The risk of vector-borne disease is often not perceived by communities.**

786 The communities do not necessarily perceive pathogen-carrying arthropods as a threat
787 that would prompt their elimination. Malaria and sleeping sickness, for example, are still often
788 perceived as supernatural diseases [101,102], making it difficult to realize the need to protect
789 oneself from vectors with nets (anopheles) or screens (tsetse flies). In some cases, the perception
790 of the vector as a cultural symbol goes beyond that of a potential disease risk associated with
791 it. For example, claiming the identity of the Camargue (southern France) also means accepting
792 mosquitoes, which only the indigenous populations of the region are able to protect themselves
793 from, despite the role of these mosquitoes in malaria or West Nile virus transmission [103].

794 **Can the risks of intervention exceed the benefits of vector control?**

795 The harmful environmental effects of insecticides combined with the emerging
796 resistance of insect vectors have exposed the need to consider less environmentally damaging
797 control methods. Genetically engineered arthropods have the potential to radically change pest
798 management worldwide. But how are they perceived and accepted by communities? People in
799 Tanzania prefer genetically-modified mosquitoes to insecticides to fight malaria, comparing
800 this technology to their own experiences in selecting desired traits in plants and domestic

801 animals through cross-breeding [104]. In Burkina Faso, people seem to be more divided on this
802 issue, stressing the need for interaction between the stakeholders [105].

803 While the ecological role of arthropod vectors in their communities is not well
804 understood, there is a growing awareness of the potential environmental impacts of vector
805 control. This awareness, in part, reflects an emerging paradigm change from anthropocentrism
806 to biocentrism in our approach to the environment. Will removing pathogen-carrying species
807 have unintended or unanticipated consequences? So shouldn't we attempt to develop ways of
808 removing pathogens from the arthropods while keeping their vectors untouched, thereby
809 running a risk of ecological damage, which is still difficult to assess today?

810 **Figure Legend**

811

812 **Figure 1. The diversity of ways in which changes in arthropod vector population size may**
813 **influence ecosystem functioning and biodiversity.** Vectors may play pivotal roles in
814 ecosystems. Besides their role in regulating animal and plant populations (through the
815 transmission of virulent pathogens), some studies suggest that the suppression of an arthropod
816 vector in an environment may alter (i) trophic interactions through both bottom-up (top left
817 ring) and top-down trophic cascades (bottom left ring), (ii) inter- and intraspecific competition
818 (top right ring), and (iii) plant pollination (bottom right ring). The top left ring features adult
819 and larval mosquitoes and the diversity of their aquatic and terrestrial predators, as well as the
820 tritrophic interactions between plants, aphids, and ladybugs (magnifying glass). The bottom left
821 ring depicts mosquito larvae which can contribute to the decomposition of organic detritus and
822 water purification by feeding on microorganisms and organic waste, and the relationship
823 between hemipteran vectors and their symbionts. In this picture, the magnifying glass illustrates
824 bacteriocytes (i.e., specialised host cells of some hemipterans containing endosymbiotic
825 bacteria). The grey arrows show the within-species vertical and the between-species horizontal
826 transmission of these endosymbionts. Solid black arrows in the upper right ring illustrate
827 competitive relationships between individuals belonging to different species (i.e., interspecific
828 competition between mosquito species and larval stages of amphibians). The grey arrow shows
829 competition between individuals of the same species (intraspecific competition). Pollination is
830 depicted by the visit of a male *Aedes albopictus* on a flower of *Felicia amelloides* (photo credit
831 Nil Rahola/MIVEGEC IRD).

832

833 **Figure 2. Vector control-mediated intraguild predation. (a)** In the absence of vector control,
834 the target species (and other non-target organisms) thrive and are preyed upon by species
835 occupying higher trophic levels (predators 1 and 2). Trophic links may also exist between
836 predators (predator 2 can represent an occasional food item for predator 1). **(b)** In the presence
837 of vector control, the abundance of target and non-target arthropods decrease. In turn, predator
838 2 abundance drops not only because of the rarefaction of its prey but also because of the
839 increased predation rate by predator 1. As one example, Allgeier et al. [10] showed that in Bti-
840 treated mesocosms, the dragonfly larvae *Aeshna cyanea* induced a 27% reduction in the survival
841 of the newts *Lissotriton helveticus* and *L. vulgaris*. High abundance of arthropod prey may
842 favour the coexistence of other prey and predators in the community by suppressing intraguild
843 predation, hence preventing food web collapse. In this figure, the number of individuals (n=3
844 in panel (a) vs. n=1 in panel (b)) represents the abundance of each species in the ecosystem, and
845 the arrow width indicates the intensity of the predation.

1 **Outstanding questions**

- 2 • Are the ecological roles of vectors redundant to those of similar non-vector organisms?
3 What are the ecological consequences of eliminating functionally-redundant vector
4 species?
- 5 • What level of scientific evidence is acceptable or required to conclude that a vector
6 species is an essential component of ecosystem function and stability?
- 7 • How do vector ecological roles vary spatially and temporally? Is there vector intra-
8 specific variability in the contribution to these ecological functions?
- 9 • To what extent can metabarcoding reveal the nature and strength of biotic interactions
10 (pollination, competitive and feeding links) occurring between arthropod vectors and
11 other community members?
- 12 • Can network analysis help to predict the ecological consequences of vector suppression?
13 And, is there a threshold in vector population size below which ecological collapse can
14 occur?
- 15 • Do pathogens quantitatively or qualitatively alter the ecological roles of their vector
16 hosts?
- 17 • How do we balance the ecological risks of vector suppression with the health risks of
18 vector-borne pathogens? And does the social perception of arthropods as pathogen
19 vectors support their elimination?

Authors's responses to reviewers' comments appear in bold font below.

Reviewer Comments:

Reviewer #1

1/ I appreciate the fact that there are very few studies on biodiversity and arthropod vectors of plant and animal pathogens, but it seems to me that this review has pushed the limits of credulity. The authors have cited publications that refer to living organisms but have claimed that arthropods specifically are important 'to clean water, and oxygen', have cited basically laboratory experiments in support of land biodiversity, etc. Sometimes there are sentences that are frankly ambiguous, e.g. the section on natural versus constructed wetlands. The authors need to re-examine the references that they cited and make sure that the reference actually supports their claim or modify their statements to be in line with the reference cited.

Authors' response: We agree with reviewer 1 and accordingly, we have ensured that the messages and ideas conveyed in each sentence of the revised version are supported by appropriate references.

2/ Major 'bones of contention' for me: 1. arthropods do not transmit disease, they transmit pathogens.

We fully agree with reviewer 1 that pathogen transmission does not necessarily cause diseases, and accordingly we made sure that this mistake has been fixed throughout the text in this revised version.

3/ more predator species (i.e. greater biodiversity) does not equate to better pest management.

We agree and the previous section "How do changes in biodiversity affect the biology of disease vectors?" is no longer included in this revised version. The part mentioned above by reviewer 1 belonged to this deleted section.

4/ Line 5, 9, 19, etc. Arthropod vectors transmit pathogens, not diseases. Whether a host (plant or animal) becomes diseased depends on a large set of factors - pathogen virulence, amount of pathogen, physiological state of host, etc., etc. This should be abundantly clear at this time of the corona virus pandemic. Correct throughout ms.

It is now corrected throughout. See also our response to reviewer 1's comment 2/ above

5/ Line 25. The use of the term 'vector' here is questionable. Bees can 'vector' pollen, but how are 'food-web links' vectored, or recycling organic waste?

We agree that the wording of this sentence was problematic. The abstract has now been extensively revised and this issue is now resolved.

6/ Line 35-38. The cited article DOES NOT state that the erosion of arthropod diversity has consequences for...clean water, and oxygen. What is actually written in that cited publication is: "Food, fuel, clean water, oxygen, disease control and other services essential for human life

are products of biological processes performed by the variety of living organisms that inhabit natural and managed ecosystems." In fact, neither the word insect nor arthropod appear in that citation.

Reviewer 1 is right, this reference was miscited (it was not specific to arthropods but to all living organisms). The introduction has been substantially revised and this sentence is no longer included in the new version of the introduction.

7/ Line 62. Insect phyla should not be put in italics, only genus and species should be italicized.

This sentence is no longer included in this revised version.

8/ Line 64-5. The re-emergence of diseases could indicate a lack of vaccination, movement of susceptible populations, or break-down in the use of, for example, mosquito nets or laxity about covering water containers. It does not necessarily indicate 'the spread of arthropod vectors'. If there are no infected hosts, it doesn't matter if the vector is present or not - there will be no pathogen transmission.*

We agree. This sentence is no longer problematic as it has been removed in the revised version

9/ Line 73. As mentioned in the previous comment, the use of physical barriers such as mosquito nets and covering water containers are neither a vaccine nor a cure for a disease.

We agree and the sentence now reads: "When control measures that directly target pathogens (vaccines, drugs) are unavailable or inefficient, vector population management can be an effective means of disease prevention (**Box 2**)" (see lines 49-51 of the revised version). Furthermore, we now provide a box that briefly describe the diversity of vector control approaches.

10/ Line 135-6. The authors mis-understood the publication cited and stated that "In ticks, abundance is greater in more diverse rodent host communities." However the publication actually reads: "The evidence for a negative effect of host biodiversity on *I. scapularis* invasion was mixed." "There were significant associations between the abundance of ticks and season, year of study and ambient temperature." "Infestations of hosts with nymphs were lower when host species richness was higher."

We thank reviewer 1 for this clarification. This part belonged to the deleted section and is thus no longer included in this revised version.

11/ Line 143-6. This section on the abundance of vector species of plant pathogens is extremely small as compared to the verbiage devoted to vectors of animal pathogens. The authors only discuss aphids and failed to mention that infected plants often support larger population of vectors species than uninfected plants. This is a very important point, and changing the landscape will not affect this phenomenon.

This part belonged to the deleted section.

12/ Line 162-3. There is a fundamental difference between an agro-ecological study and actual pest management. While there may be more predatory species available in a more biodiverse environment, that does not mean that there will necessarily be greater pest management because these 'additional' predators are quite often preying on non-pest species, species that may be entirely neutral to the crop system. Biodiversity does not equate to greater or better pest management. Parasitoids, for example, are often host-specific and to manage a pest, specific parasitoids need to be present.

This part belonged to the deleted section.

13/ The effect of predators, which may be more generalized in prey feeding, is more difficult to determine because often no host remains are left. Additionally many studies the predator abundance and/or diversity was never linked to pest management. See Furlong and Zalucki review Exploiting predators for pest management: the need for sound ecological assessment.

This part belonged to the deleted section.

14/ Species interactions: See comments above: more predators does not necessarily mean better vector management, effect of infected plants on increased vector populations, etc.

This part belonged to the deleted section.

15/ Line 211-2. The tick experiment was a 15 cm microcosm = petri dish trial. This shouldn't be included when talking about landscape/open fields/biodiversity. Laboratory trials are often notorious for producing results different from actual field results.

This part belonged to the deleted section.

Reviewer #2

1/ This manuscript is a review of the literature and discussion of animal and plant pathogen vector biodiversity. It comes at a very critical time when there is global discussion about drops in arthropod numbers and diversity, new control methods that have a capability of "surgically" removing a small subset of unwanted vector species, and a new area of studying and eventually understanding whole ecosystems. Of course, the emphasis is on animal and human pathogen vectors because of the critical impact these arthropod species have on livestock and human health and because so much literature has been devoted to these med vet arthropods. However, I would point out that these same issues and concepts could be argued to be equally important to the understanding of the ecology of phytopathogen vectors. I am a bit surprised that there wasn't more supportive information or pointing out of gaps in surveillance for these vectors, especially since at least two of the authors are well known phytopathogen vector researchers! There is actually quite a bit of literature that would be great to include in this paper if you had the time and room to devote to inclusion of some of this material. For example, a quick library database search of "leafhopper biodiversity" and then a subsearch of "vector" came up with several references to leafhoppers critical to grassland, orchard, and cropping ecosystems. Some papers even discussed the danger of

lowered biodiversity and how it is changing leafhopper vector-plant host dynamics - something that you spend some time on in your review.

In short, I appreciate the value of your manuscript and enjoyed reading it very much, but I found it a bit lopsided towards mosquitoes especially considering that there IS a lot of information on the plant side to support your arguments. I would suggest a more balanced approach, if possible.

Authors' response: We are very grateful to reviewer 2 for her/his comments and for pointing out this literature that we had missed. All reviewers mentioned that the manuscript failed in being balanced, and many sections were underdeveloped. We agree and we have added many more non-mosquito examples to this revised version. More generally, we paid particular attention to a better balance between examples from human, animal and plant pathosystems.

Regarding the role of leafhoppers, we found some of the papers we believe are the ones highlighted by Reviewer 2:

- Rowe and Holland (2013) High Plant Richness in Prairie Reconstructions Support Diverse Leafhopper Communities. *Restoration Ecology*
- Helbing et al. (2021) Restoration measures foster biodiversity of important primary consumers within calcareous grasslands. *Biological conservation*.
- Primi et al. 2016 From Landsat to leafhoppers: A multidisciplinary approach for sustainable stocking assessment and ecological monitoring in mountain grasslands. *Agriculture, Ecosystems and Environment*.

These references are highly relevant to our previous section 1 "how does biodiversity influence vector ecology". This section is no longer included in the ms., which now exclusively focuses on the ecological roles of arthropod vectors. Concretely, in addition to provide more examples of plant pathosystems throughout the revised text, in the "bottom-up trophic effects" section, we have specifically added the example that reviewer 2 develops about the lesser prairie chicken (see reviewer 2's comment 13/ below). In particular, we have added at lines 140-144: "Likewise, leafhoppers, including several key vector species like *Macrostelus quadrilineatus* and *Graminella nigrifrons*, can represent a significant part of the diet of the endangered lesser prairie chicken. Elimination of these abundant vector species, which are indicators of grassland habitat health, may have unintended consequences to its predators and destabilize the foodweb dynamic [28]".

With ref 28 : Rowe and Holland (2013) High Plant Richness in Prairie Reconstructions Support Diverse Leafhopper Communities. *Restoration Ecology*

However, we have not been able to find references that support the sentence about the importance of leafhopper as a food resource for the lesser prairie chicken. Rowe and Holland wrote in the conclusion section of their paper: "Leafhoppers can account for a significant proportion of aboveground insect biomass and are prey to many other vertebrates and invertebrates, therefore their abundance and diversity can indicate quality grassland habitat. Our findings indicate that establishing high richness restorations pays off in terms of creating a foundation to support animal food webs".

We would be very grateful if reviewer 2 could recommend an appropriate reference supporting the food reliance of prairie dog on leafhoppers. Furthermore, other leafhopper examples are mentioned at lines 144-149 and 152-155.

Specific comments:

2/ Line 5. insects transmit disease pathogens, not diseases

We fully agree and this has been fixed throughout (see also answers to reviewer 1's comment 2/ and 4/ above).

3/ Line 59. insects transmit viruses and bacteria; vector is a noun, not a verb

Agreed and in this sentence the word "vector" has been changed to "transmit" see line 42 of the revised version

4/ Line 74-77. These two sentences in pink are a little shaky. Could you expand a bit here to make the logic flow better?

We agree and this section on vector control has been revised and expanded to make the logical flow clearer (lines 49-61). In addition, in this revised version, we now provide a new box on vector control tools (box 2, see also reviewer 3's comment 4/).

5/ Line 92. I like your introduction and outline of how you will present your arguments linking to the One Health concept.

We thank reviewer 2. In this revised version, we provide more examples derived from the plant literature. Likewise, we have better highlighted how the developed examples could echo the One Health concept (e.g. see lines 172-174 and lines 300-301).

6/ Line 99. Just a suggestion, but you may want to direct the reader to the Glossary again for these definitions. Happy to see you discuss the different "categories" or definitions of biodiversity. Helps the reader to understand the complexity of the issue you address.

The whole previous section " How do changes in biodiversity affect the ecology of disease vectors?" has been removed in this revised version. The part mentioned by reviewer 2 belonged to this deleted section. However, we have added the definition of biodiversity and its different categories in the revised glossary.

7/ Line 120. Because you contrast with an example from Thailand in the next sentence, you may want to provide information about where this study (ref #19) was conducted. In the US? France? Sorry, I didn't look it up.

This part belonged to the deleted section.

8/ Line 130. You make a nice statement that reduced resources may impact vector diversity and give the example of increased management of forests associated with reduced fly vectors. But, you leave me hanging! What did the paper say about which resources were reduced or

managed? Were these flies blood feeders and was increased management associated with reduced mammalian or other host species? If you have room, please expand here.

This part belonged to the deleted section.

9/ Line 146. Only a single citation for this statement? This is a very active area of research and there must be more out there. Please look for additional citations to strengthen this statement and to better support your overall conclusions.

This part belonged to the deleted section.

10/ Line 153. Yes! This is a critical point that you bring up, but your statement is supported by examples of human and animal pathogen vectors, no plant pathogen vectors. I would argue that this statement is critical for BOTH. Please dig into the literature to come up with examples (or lack of examples) that demonstrate this crucial gap in knowledge about phytopathogen vector competence and just how much we do not yet know.

This part belonged to the deleted section.

11/ Line 439. differs should be differ

This has been fixed.

12/ Line 849. improper word use: should be disease pathogen vector

The size of Box 3 has been reduced and this part is no longer included.

13/ Line 862. one aspect that might add to this section is the value that insects, including vector species, represent as food or as a vital part of the food web (that you already mentioned). For example, in prairie ecosystems, leafhoppers (which include several key vector species like *Macrostelus quadrilineatus* and *Graminella nigrifrons*) are used as a measure of ecosystem health, much in the way that stream ecologists use aquatic insect naiads to determine health of bodies of water. One interesting factoid is that the endangered lesser prairie chicken consumes leafhoppers as a main part of its diet. Elimination of these abundant vector species may have unintended consequences to the lesser prairie chicken.

We agree and we now mention this specific example of leafhopper in the section “bottom-up effects” at lines 140-144 (see also response to reviewer 2’s general comment 1/ above). We also added the food value dimension in the Box 3 at lines 780-782 which now reads: “Some arthropods are viewed positively for their aesthetic value (e.g., butterflies and dragonflies), as symbols of good luck (e.g., ladybugs), and others for their usefulness as pollinators (e.g., honeybees) or protein source (e.g., migratory locusts)”

14/ Line 889. Interesting!!

Reviewer #3

1/ The authors have taken on a big and important topic, and present many interesting examples. Unfortunately, I found this article not so helpful to me and I think it may be because the authors took on such a broad range of topics without presenting in a reproducible way how they chose those examples. Within the areas where I have some familiarity with the literature, I notice important gaps in the authors' coverage of the literature, which make me think it may not have been possible for the authors to do a systematic search of the literature while covering so much ground. I think the manuscript would be strengthened by narrowing the scope and providing information about how the authors searched the literature and selected examples, as in a systematic review.

Authors' response: We fully agree with reviewer 3. All reviewers mentioned that the manuscript failed in being balanced, and many sections were underdeveloped. We have restricted the scope of the review, which now focuses on the previous section 2 "How do changes in vector abundance affect surrounding biodiversity? This freed up space for more examples, including many non-mosquito examples to this revised version. More generally, we paid particular attention to a better balance between examples from human, animal and plant pathosystems.

2/ It is not clear to me whether the authors are including in "ecology" only abundance or also other aspects important to disease ecology such as infection prevalence in vectors.

The whole previous section " How do changes in biodiversity affect the ecology of disease vectors?" has been removed from this revised version. The part mentioned by reviewer 3 belonged to this deleted section

3/ This article would be strengthened by addressing the mechanisms by which biodiversity influences vector ecology. For example:

Line 139. "Increasing vegetation cover and size of wood ant nests also reduce Ixodes tick abundance at the larval stage [34]. Consistently, larval Ixodes tick abundance was lower in ant-infested than control sites; however, the abundance of nymphs was higher in presence of ants [35]."

This summary of past studies seems to be missing important context about ***why*** wood ant nests may influence Ixodes tick abundance. What did the authors of those cited studies say about why they saw the effects they saw? For example, did they find evidence for, and pose hypotheses, about effects of ants on ticks via microhabitat change, predation, etc? What unanswered questions remained for those studies?

This part belonged to the deleted section.

4/ This manuscript would be strengthened by the authors making it a systematic review following PRISMA standards (<http://www.prisma-statement.org/>). As written, it is generally unclear whether the authors' choice of examples reflects a systematic search of the literature, examples that the authors found most interesting, or based on some other criteria. A systematic review would enable the authors to draw qualitative and quantitative conclusions about, for example, where (taxa, geography, direction of effect, type of interaction) there has been more or less study effort. This evidence would enable the authors to point to gaps and

unanswered questions in ways that I do not think are possible with the current approach. For example:

Line 225. "...data that are unavailable for most taxa. The examples described below are derived primarily from mosquito studies. There is an urgent need to determine how ecosystems are affected by changes in the abundance of other vector species."

Without information provided in the paper about how the authors searched for studies (as in a systematic review), it is not possible to know what studies are available for taxa other than mosquitoes. For example, winter ticks (*Dermacentor albipictus*) cause mortality in moose *Alces alces* (e.g. Debow et al. 2021 <https://wildlife.onlinelibrary.wiley.com/doi/full/10.1002/jwmg.22101>), and this long-recognized effect seems an example of a vector other than mosquitoes affecting biodiversity at least with respect to moose and likely with knock-on effects for plants that moose eat and predators of moose. I understand that a systematic review may be outside the scope of this review; that said, I think the reader needs more information throughout about how the authors searched the literature (i.e. search terms used) and how they chose examples. If the authors did choose to take on a systematic review, then this might be made more feasible by narrowing the scope of the paper, for example by vector taxa or geography. Here is another example of how lack of information about how the authors found and chose examples may result in an incomplete picture of the complexity and range of vector interactions with biodiversity.

As space has been freed up by the removal of previous section 1, more examples have now been added in this revised version, including a new paragraph dedicated to direct top-down trophic effects of adult arthropod vectors on the population dynamic of their vertebrate or plant hosts. The winter tick is a perfect illustration and Debow et al. 2021 is now cited at lines 192-194 (see also lines 197-200 for another example on the tick *Amblyomma americanum*). Generally, we have added more non-mosquito examples throughout to get a better balance between examples. We would also like to point out that review articles in Trends in Parasitology do not have the objective to present a comprehensive review of the existing literature as systematic reviews do. Rather it "offers a balanced account of newly emerging or rapidly progressing fields and provide a guide to the most relevant recent literature (concentrate on the seminal references of the past 2–4 years) and prospects for future research". This being said, in order to make sure not to miss such recent seminal articles, we have, as part of the revision of this article, proceeded to a systematic search in Web of Science with the following strings in the field "Topic" or "Abstract" and date range (last 5 years).

Vector OR mosquito OR tick OR flea OR bug OR blackfly OR sandfly OR tsetse OR midges OR hemipteran OR aphid OR whiteflies OR thrips OR leafhoppers OR planthoppers OR plant-lice OR spittlebugs

With the subsearch (AND): foodweb OR competition OR pollination OR predator OR prey OR trophic interaction

Similar searches were repeated using arthropod scientific names.

5/ Line 135. "In ticks, abundance is greater in more diverse rodent host communities"

This is a relevant example with one direction of effect of biodiversity on vector abundance. By contrast, other studies in other ecosystems have found effects in the opposite direction. For example, increased rodent abundance correlated with reduced current-year questing *Ixodes scapularis* abundance (presumably due to more ticks being on rodents rather than question), while presence of more diverse predator communities reduced infection prevalence for nymphs (Ostfeld et al. 2018: <https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/ecy.2386>)

This part belonged to the deleted section.

6/ In some places I was confused about whether all of the examples were about vectors. For example:

Line 272. “The well-known plant-aphid-ladybug interaction is illustrative, where reduction in aphid biomass can have significant bottom-up effects on predatory ladybugs, not only at a field scale but also at the landscape level”.

Are aphids always vectors, or principally affecting plants as vectors, or are some aphids simply plant predators?

This is a very good point. No, not all aphids are pathogen vectors. Some hemipterans cause direct damage (pests) only, while others both cause direct (pest) and indirect damage (through the transmission of virulent pathogens). We made this distinction at lines 202-209. We have focused here on pathogen vectors except on two occasions: the giant willow aphid *Tuberolachnus salignus* (see lines 165-167) and *Aedes nigripes* the most abundant arctic mosquito (see lines 230-233). To our knowledge these species do not transmit any virulent pathogens to their hosts, but we would like to point out that these fundamental study models may reveal ecological roles relevant for other systems of health importance.

7/ In places the paper would be clarified by addressing where in the world the statement fits. For example:

Line 347. “A similar pattern of species displacement by a superior competitor is seen with the invasive Asian blue tick *Rhipicephalus microplus*, the main vector of *Babesia*, which is currently displacing many indigenous *Rhipicephalus* species in tropical regions [95].”

Ixodes scapularis is the main vector for *Babesia* in North America.

We agree and when possible we now precise where geographically the statements fits (Kenya line 100, USA line 106, Thailand line 127, Sweden line 129, South Africa line 135, North America line 154, 198, 269, La Réunion Island line 158, New Zealand line 165, Camargue line 791, etc.. In particular *Rhipicephalus microplus* is the main vector of *Babesia* in tropical regions (line 274).

8/ There are aspects the authors bring up but do not give sufficient attention to offer insight for the reader. For example:

Line 411. “The use of novel technologies suppressing or eliminating vector populations has immense potential but poses significant ecological, environmental, societal, and ethical questions [112].”

The authors briefly mention novel technologies but do not address it in depth, therefore mentioning it in the conclusion does not seem to represent well the rest of the paper. Suggest going more in depth or defining scope to exclude topics that cannot be given more attention.

We fully agree and now provide a full box on this topic (BOX 2 “A brief overview of the diversity of vector control tools”). See also answer to reviewer’s 2 above.

10/ There do seem to be at least some important gaps in the paper that may point to the benefits of narrowing the scope so as to give fuller attention to fewer topics. For example: Line 196. “Interactions with microbes (bacteria, fungi, viruses, and protists) also play a role in the biology and ecology of vectors.”

This paragraph addresses endosymbionts of vectors. Missing from this paper, however, is discussion the role of ***naturally occurring*** entomopathogenic microbes, separate from human-applied biopesticides like Bti that the authors do mention.

Although this section has been removed from this revision, we agree that the scope was too broad and did not allow for appropriate development of certain aspects. In this revised version, we now give more attention to fewer topics by focusing on the ecological roles of arthropod vectors. Regarding endosymbionts and naturally occurring entomopathogenic organisms, we now dedicate a specific paragraph to the microbiome (see lines 222-226) and we have added it to the glossary.

Figure 1

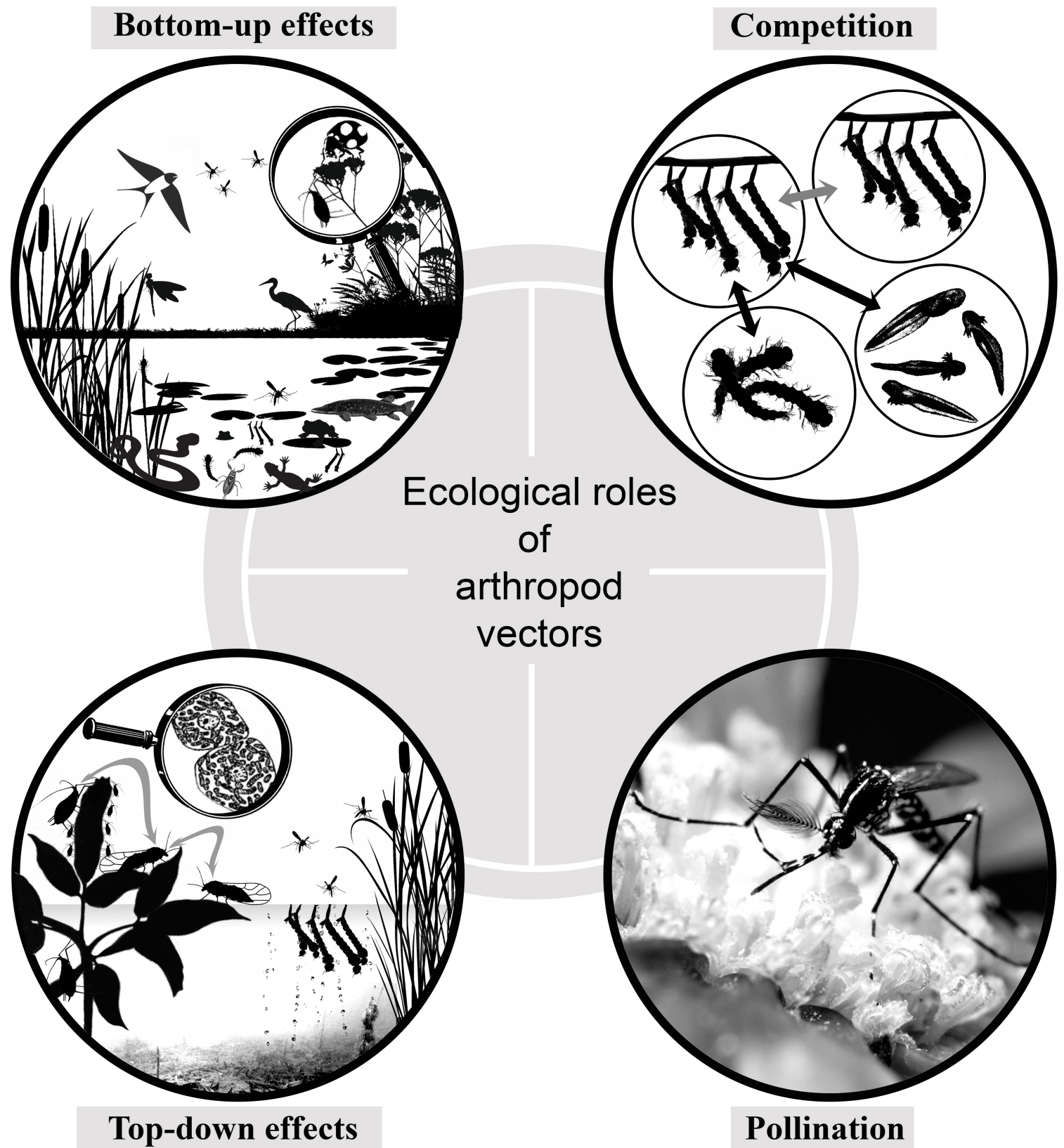
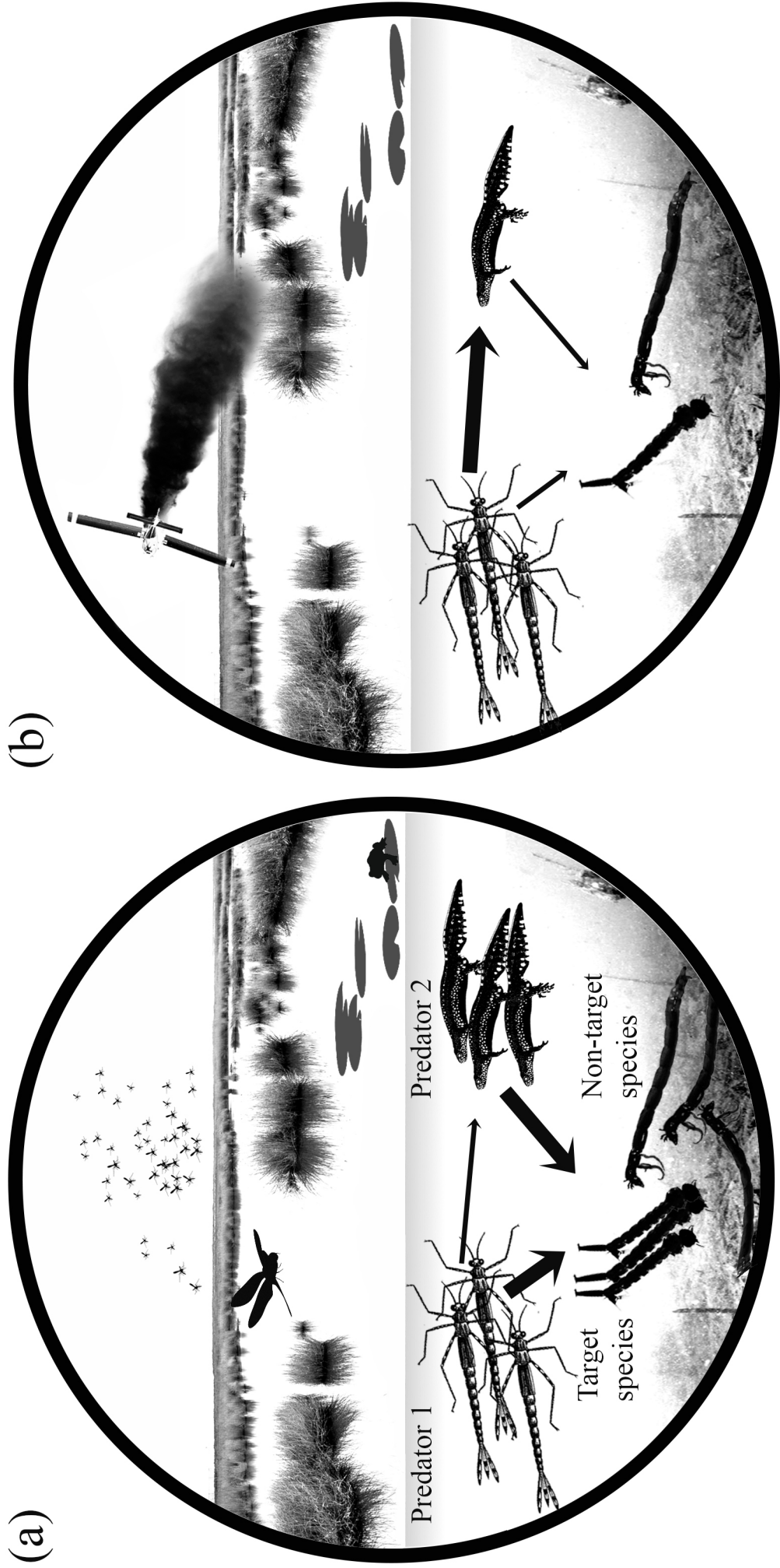


Figure 2



Box 1



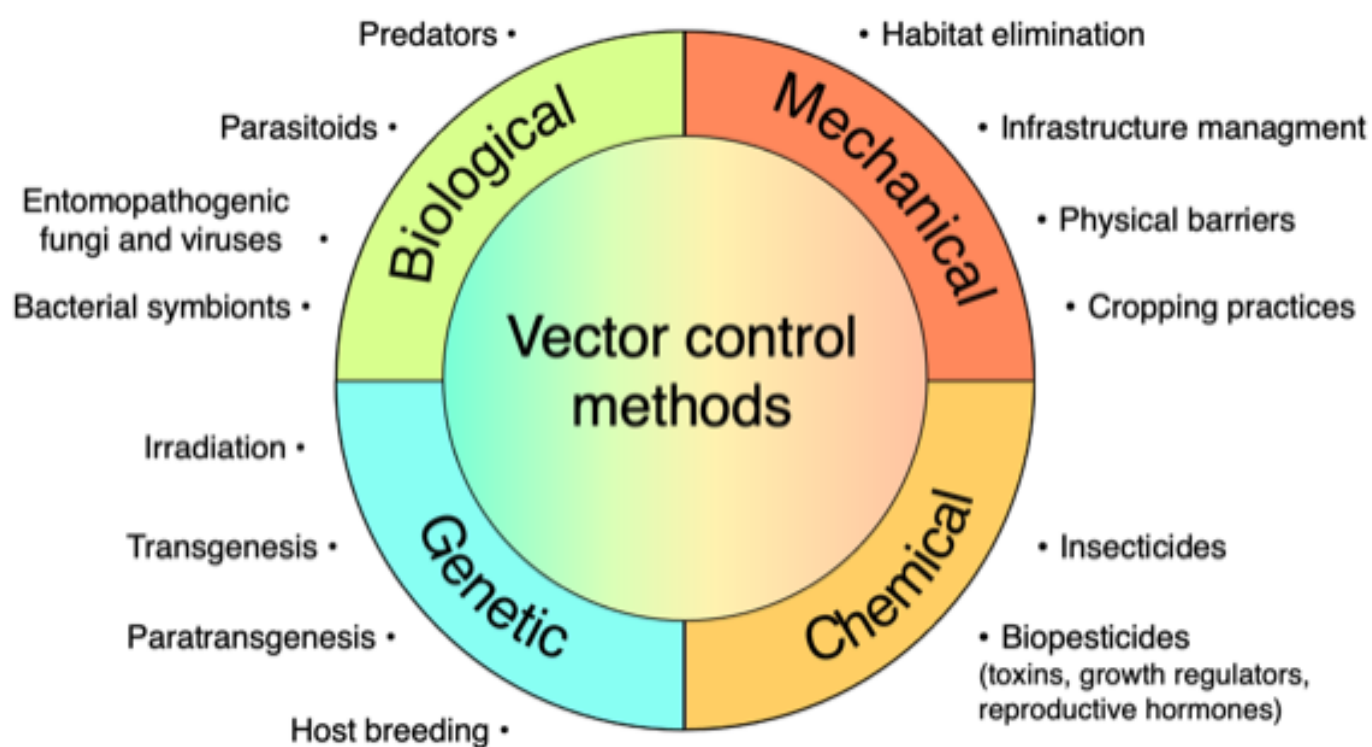
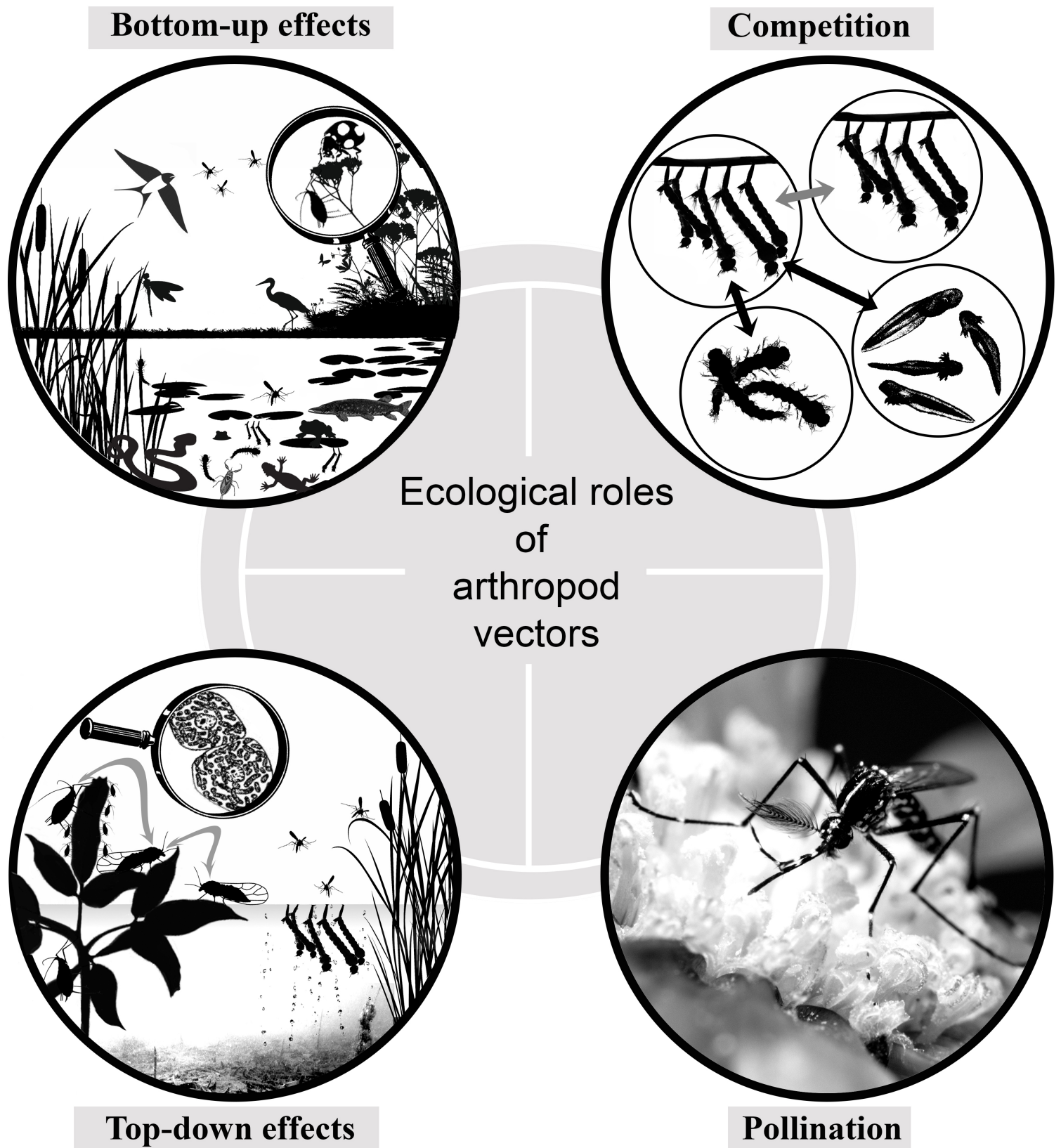
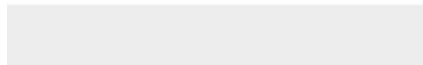
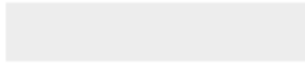


Figure 1





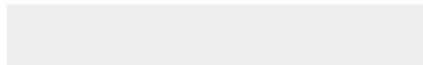
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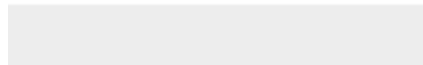


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