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

Thierry Lefèvre, Nicolas Sauvion, Rodrigo P.P. Almeida, Florence Fournet, Haoues Alout

Highlights

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

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Keywords: Ecosystem functioning, biodiversity, arthropod vectors, plant, animal, human

Abstract

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

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

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

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

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

Food web links

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

Bottom-up effects

Arthropod-vector control, and collateral reductions in non-target species, may impact predators that rely on these species for food. A recent dietary analysis of arthropod species present in the faeces of western bluebirds in California vineyards revealed that *Aedes* spp. was by far the most common item recovered, occurring in 51.2 and 49.1% of samples from adult and nestling, respectively [8]. Furthermore, studies are beginning to examine the effects of vector control on the food webs in which they reside. For example, long-term field monitoring and mesocosm experiments following mosquito control with the larvicide *Bacillus thuringiensis* var. *israelensis* (Bti) have revealed largely negative consequences of the Bti-induced reduction in mosquito density (along with reductions in non-target chironomids). These effects include reductions in the abundance, size, or diversity of aquatic and terrestrial predators, including dragonflies and damselflies [9], newts [10], frogs [11], and birds [12]. Therefore, reductions in mosquito density or non-target species may affect predators and have cascading effects on other trophic links (**Figure 2**).

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

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

Similar considerations may apply to other Dipteran-vector species. While the predators of sandflies, midges, black flies, and tsetse flies are less well known than that of mosquitoes, a diversity of aquatic and terrestrial predators, including hydra, moths, spiders, ants, crickets, odonatan, other Diptera, fish, and birds, feed on the larvae and adults of these vectors [21–24]. The predation is likely density-dependent with substantial spatial and temporal variation in the contribution of these vectors to the diet of their predators. At very high densities, these insects could even be prime candidates for human entomophagy, as has already been observed in Thailand [25]. Dejections of arthropod larvae in their aquatic habitats can also be an essential resource for many microorganisms and contribute to soil fertilization. For example, blackfly dejections drifting in Sweden streams and rivers can reach 429 tons per day, or as many as 6000 elephants defecating each day [25].

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

While most predators of animal and human pathogen-vectors seem to be generalists, predator-vector or parasitoid-vector relationships within plant systems tend to be more specific. 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 [28]. Likewise, leafhoppers, including several key vector species like *Macrosteles quadrilineatus* and *Graminella nigrifrons*, can represent a significant part of the endangered lesser prairie chickens' diet. Elimination of these abundant vector species, which are indicators of grassland habitat health, may have unintended consequences on their predators and destabilize the food web dynamic [29]. The aforementioned DNA metabarcoding analysis in California vineyards found that a significant proportion of the western bluebird diet was composed of Hemipteran vectors of plant pathogens, including *Aphis craccivora*, a vector of numerous plant viruses and the leafhopper *Graphocephala atropunctata* (formerly *Hordnia circellata*), the most important vector of *X. fastidiosa* that causes Pierce's disease to grapevines in coastal California [8].

Hemipteran populations can be regulated by parasitic wasps (i.e., parasitoids), which often have a narrow host species range. Eliminating or reducing hemipteran vectors may limit the long-term maintenance of parasitoid populations, resulting in biodiversity loss. For example, the abundance of the *Anagrus* spp. parasitoids decreased when the density of *Erythroneura* spp. leafhopper-hosts, a serious pest to grapes in North America and a suspected vector of viruses and phytoplasma, decreased [30] (see also [31,32] for similar examples of specialist parasitoids of tsetse flies and ticks). However, in some cases, a decrease in target vector density can be compensated by host switches to related non-vector host species. For example, in La Reunion island, the successful eradication of the introduced psyllid vector *Diaphorina citri* by a released parasitoid was facilitated by the presence of a native psyllid that served as an alternative host for the parasitoids when the vector populations declined [33]. Diniz et al. [34] showed that the release of parasitoids in areas bordering commercial citrus groves (e.g., abandoned or organic groves, residential trees, etc.) had the potential to maximize actions for *D. citri* control.

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

Top-down effects

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

Arguably the most important top-down trophic effect of vectors is the regulation of the population dynamics of their vertebrate and plant hosts and the resulting impact of hematophagy and phytophagy, respectively (irrespective of pathogen transmission). Effects on host morbidity and mortality and changes in host behaviour in response to pervasive vector feeding can alter food web dynamics and cascade through the entire ecosystem. For example, heavy tick and flea infestations, as well as black fly outbreaks, are particularly associated with these direct detrimental effects on host populations [43–46]. However, this may not always be the case [47]. Under natural conditions, control of these hematophagous vectors could lead to host population growth with consequences on other trophic levels (e.g., increased prey abundance for carnivorous predators). As one example of a behavior-mediated trophic cascade, a study in North America found that herbivorous mammal hosts can perceive the risk of tick infestation and avoid grazing in areas with a high density of the tick *Amblyomma americanum* [48], thus possibly generating spatial variability in primary production (i.e. decreased level of herbivory pressure in tick-abundant areas).

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

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

Inter- and intra-specific competition

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

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

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

Interspecific competition can play key roles in the population dynamics of plant-pathogen vectors. Such competition can have important implications for vector management. For example, the cultivation of transgenic Bt cotton has favored the tarnished plant bug *Lygus hesperus*, a key agricultural pest in the western United States and the vector of *Pantoea ananatis* and *Serratia marcescens*, over its more Bt-susceptible Lepidopteran competitors [68]. A recent study found that interspecific competition can even be mediated by the pathogen being transmitted [69]. For example, the barley yellow dwarf virus can enhance the thermal tolerance of its vector, the aphid *Rhopalosiphum padi*, allowing it to expand its ecological niche to warmer regions and escape competition from another aphid, *R. maidis*, which is native to colder regions [69]. Interspecific competition between two vector species can sometimes affect higher trophic level. In a recent study, the presence of the thrip vector *Frankliniella occidentalis* directly reduced the performance of its competitor, the aphid vector *Myzus persicae*, but the thrip's aggregation hormone repelled an aphidophagous hoverfly [70].

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

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

Pollination

The vast majority of angiosperms rely on arthropods for pollination. In addition to bees, many flies are important plant pollinators, including of crops [80]. Thus, dipteran vectors may be providers of this valuable ecosystem service. Mosquitoes, blackflies, sandflies, and biting midges frequently visit flowers to harvest nectar for energy, although it is unknown if these visits facilitate pollination. Most information on the contribution of vectors to pollination has been anecdotal, an exception being the ceratopogonids, whose key role as pollinators of the cacao tree is relatively well described [81]. However, most ceratopogonid pollinators belong to the genus *Forcipomyia*, which is not considered a pathogen vector (but see [82]). The ceratopogonid vectors in the genus *Culicoides* are generally considered poor pollinators. However, *C. parensis*, a vector of the Oropouche virus, and *C. insignis,* a vector of Bluetongue virus, can pollinate hevea and cacao trees, respectively [83]. Maintaining diverse and abundant larval breeding sites for pollinating midges in cacao fields has been proposed as a strategy for increasing cacao yields. However, these breeding sites can be shared with larvae of *Anopheles*, *Culex*, and *Aedes* vectors [84] and may have the unintended consequence of increasing pathogen transmission. Thus, the removal or creation of these breeding sites must be considered within a one-health perspective.

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

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

Other ecological roles

The mere presence and abundance of a vector species in a habitat can protect it from human activities, thereby limiting some of the key drivers of global biodiversity loss. For example, tsetse flies and trypanosomiasis prevent the expansion of livestock farming to wild areas and prevent conflicts between humans and lions [91]. Likewise, the nuisance of mosquitoes, midges and blackflies curtail human activities in regions where they reach high densities.

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

Concluding Remarks

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

Vectors will likely exhibit weak links with other organisms in the network of interactions in their ecological community: they are neither the only resource for their predators nor the only consumer of their prey. Similar **functional redundancy** may characterize the role of vectors as pollinators. As such, if the ecological roles of vectors within an ecosystem are redundant with non-vector species, then there may be a legitimate ecological argument supporting their suppression or elimination. However, research suggests that even the elimination of weak nodes in an ecological network may result in collapse and biodiversity loss [20]. Species interactions are so complex when considering weight coefficients of the interactions that it becomes difficult to predict the consequences of removing a node on ecosystem functioning [98]. In addition, two species can be redundant on well-known traits (e.g. diet, mobility) but differ in other traits (e.g. difference in phenology or micro spatial habitat use) with consequences on interacting species (predators, competitors, prey). Suppression or elimination of a vector species does not guarantee a similar compensatory gain in the biomass of the presumably functionally equivalent species because specific rate-limiting growth factors such as temperature, may be different.

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

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

Acknowledgements

The development of the ideas presented in this review was prompted by discussions held at meetings organised by the KIM RIVE (key initiative "risks and vectors," Montpellier University). We thank Pierrick Labbé and Kurt McKean for their fruitful comments.

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Glossary

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

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

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

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

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

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

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

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

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

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

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

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

Important dipteran vectors of human and animal pathogens (**Figure I**) include *Culex pipiens* (a), which transmits arboviruses and lymphatic filariasis (LF); *Aedes albopictus* (b), which transmits Dengue, Chikungunya, Zika, and Yellow fever viruses, and LF; and *Anopheles gambiae* (c), which transmits *Plasmodium* parasites, LF and viruses. Other dipteran vectors include sandflies such as *Phlebotomus perniciosus* (d), which transmit *Leishmania*; the black flies *Simulium spp.* (e), which transmit onchocerciasis; the biting midges such as *Culicoides* *nubeculosis* (f), which transmit the Bluetongue virus; and the tsetse such as *Glossina palpalis gambiensis* (g), a vector of human and animal African trypanosomes. Triatomine such as *Triatoma sanguisuga* (h) are vectors of *Trypanosoma cruzi*. The Siphonaptera (fleas) such as *Pulex irritans* (i) are vectors of the bacterium *Yersinia pestis*. Ticks such as *Ixodes scapularis* (j) can transmit bacteria *Anaplasma* or *Borrelia* causing Lyme disease, Babesia, and viruses causing African swine fever or Crimean-Congo hemorrhagic fever. The majority of vectors of plant pathogens are hemipterans, including psyllids such as *Cacopsylla pruni* (k), vector of phytoplasma; whiteflies such as *Bemisia tabaci* (l), which transmit geminiviruses; aphids such as *Acyrthosiphon pisum* (m), vector of pea enation mosaic virus; mealybugs such as *Planococcus ficus* (n), which transmit grapevine leafroll ampelo viruses; leafhoppers such as *Homalodisca vitripennis* (o), vectors of *Xylella fastidiosa*; planthoppers such as *Nilaparvata lugens* (p), which transmit two viruses, rice ragged stunt virus and rice grassy stunt virus; and spittlebugs such as *Philaenus spumarius* (q) which can transmit *Xylella fastidiosa* in Europe. Three other taxa also play significant roles in the transmission of pathogens to plants: the heteropterans such as *Leptoglossus zonatus* (r), transmitting the trypanosomatid *Herpetomonas* infecting corn; thrips such as *Frankliniella occidentalis* (s), which transmit tospoviruses; and chrysomelids such as *Cerotoma trifurcata* (t), known to transmit bean pod mottle virus to beans. Each panel is named after the minimum taxonomic unit (super-family, family, sub-family, or genus), within which arthropod vectors can be found. For example, panel (g) is named after the genus *Glossina* because African Trypanosomes are transmitted by several species belonging to this genus. In contrast, panel (i) is named after the subfamily Triatominae because *Trypanosoma cruzi* can be transmitted by different genera (*Rhodnius, Triatoma, or Panstrongylus*) in this sub-family. Likewise, panel (k) is named after the super-family Psylloidea because vectors can be found in two families (Psyllidae, Triozidae).

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

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

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

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

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

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

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

Genetic control includes methods of vector genome modification and the release of large numbers of males, either to sterilize and suppress vector populations or to replace natural populations by pathogen-resistant vectors. Irradiation-induced DNA damage renders males sterile, which can reduce reproductive output when females mate with these males. CRISPR technology allows for precise genome modifications of vectors (transgenesis) or important vector symbionts (paratransgenesis). CRISPR technology also facilitates gene-drive systems that promote the rapid spread of the introduced mutations through the population. Breeding approaches are also a form of genetic control and consist of selecting plant genotypes that are resistant to the pathogen or the vector.

Figure I in Box 2.

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

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

Perceptions of arthropods

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). However, in general, they are perceived as nuisances and even as existential threats. Therefore, it would not be surprising if people were more willing to eliminate them than to preserve them.

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

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

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

The harmful environmental effects of insecticides combined with the emerging resistance of insect vectors have exposed the need to consider less environmentally damaging control methods. Genetically engineered arthropods have the potential to radically change pest management worldwide. But how are they perceived and accepted by communities? People in Tanzania prefer genetically-modified mosquitoes to insecticides to fight malaria, comparing this technology to their own experiences in selecting desired traits in plants and domestic animals through cross-breeding [104]. In Burkina Faso, people seem to be more divided on this issue, stressing the need for interaction between the stakeholders [105].

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

Figure Legend

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

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

Outstanding questions

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

<u>Authors' response</u>: 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 petter 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.

<u>Authors' response</u>: 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 *Macrosteles 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 Macrosteles 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.

<u>Authors' response</u>: 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 artic 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.

Figure1

Figure 1

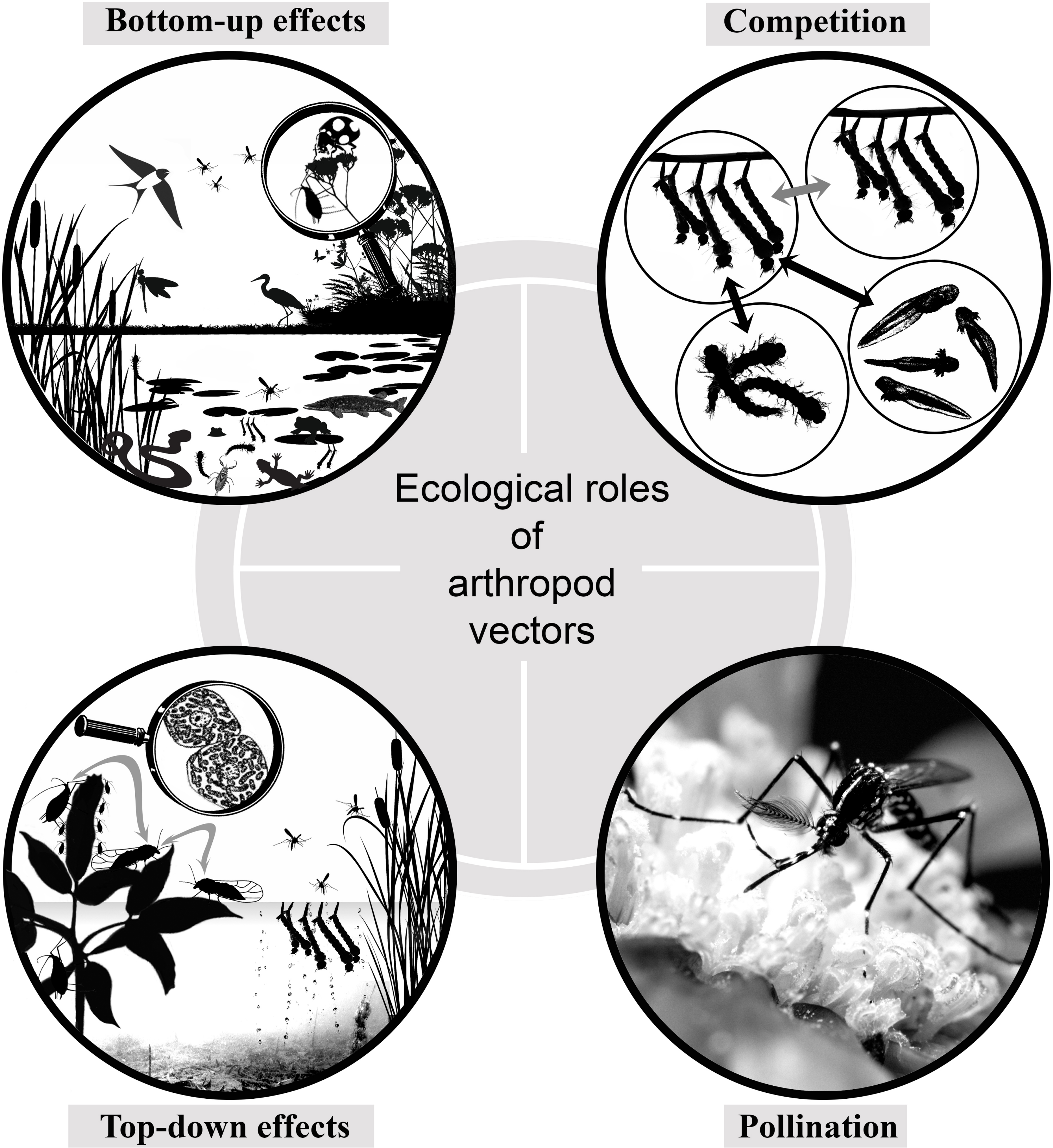
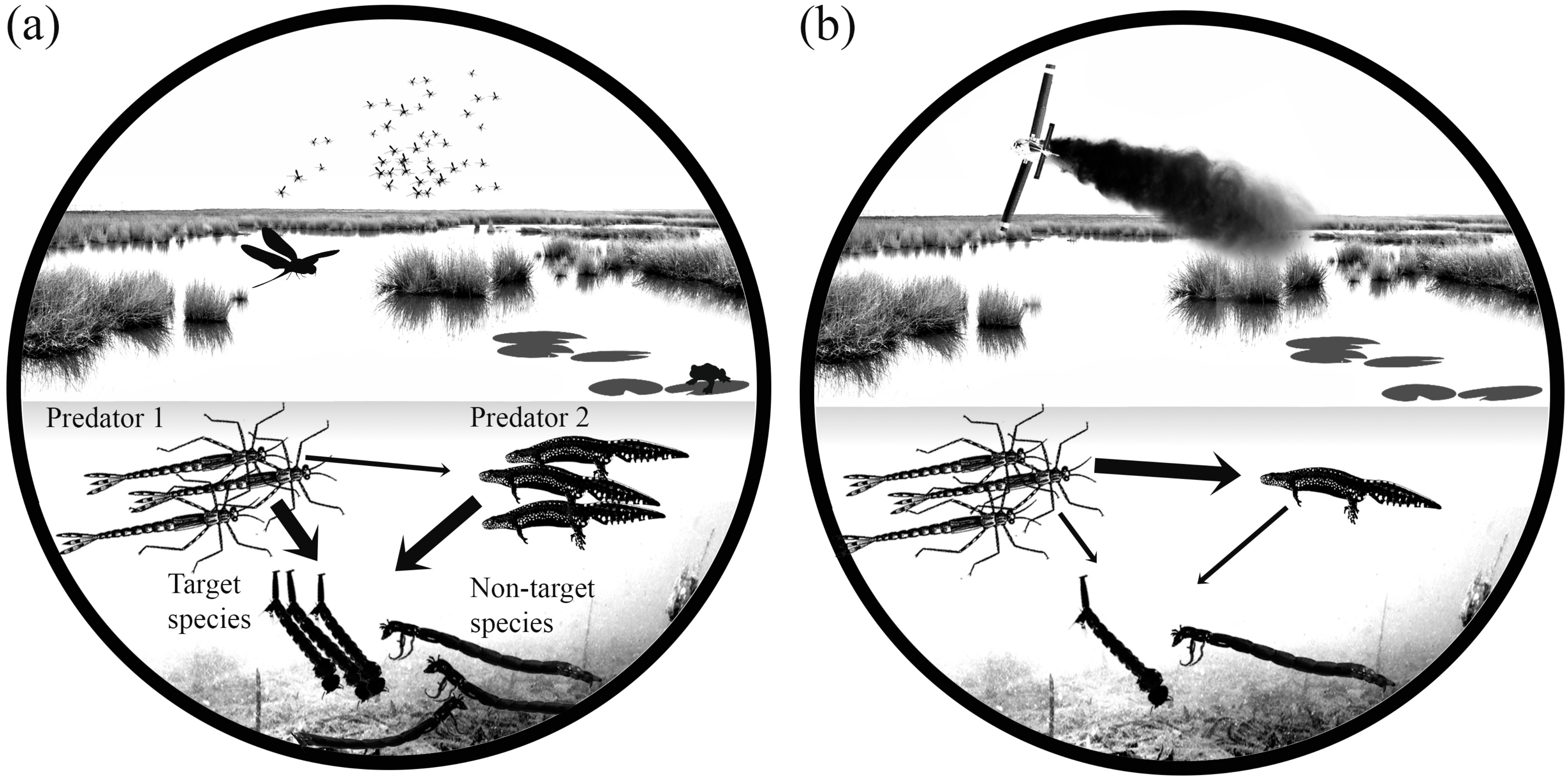
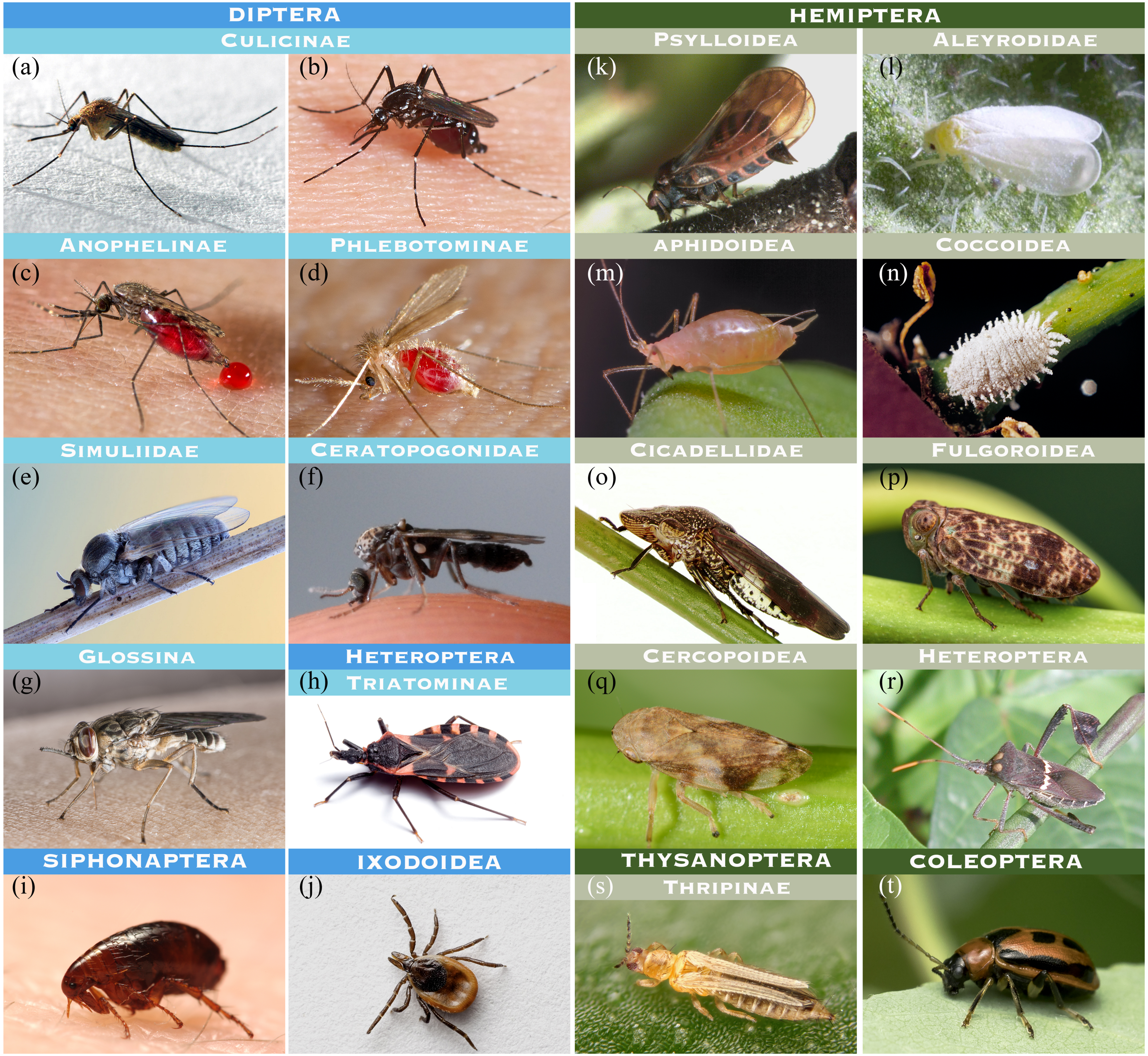


Figure 2



Box 1


DIPTERA
HEMIPTERA
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FigureI_box2

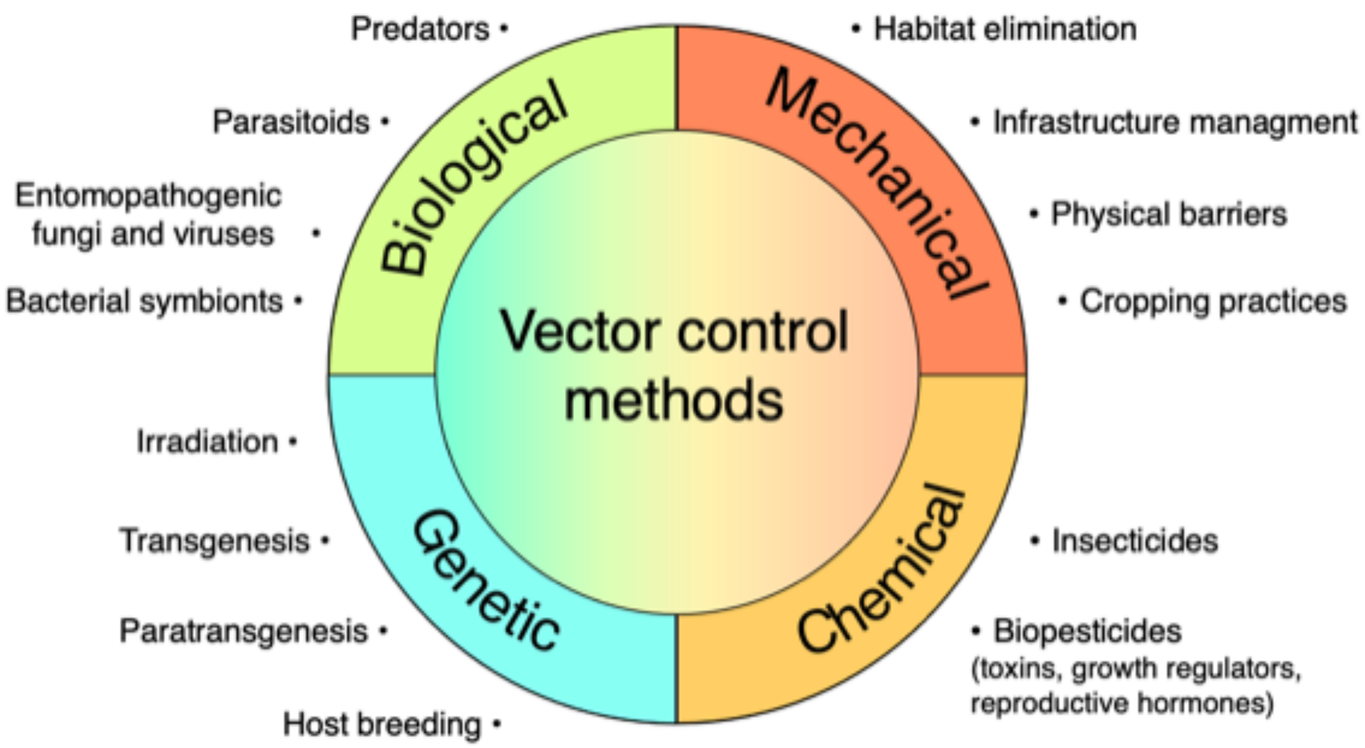
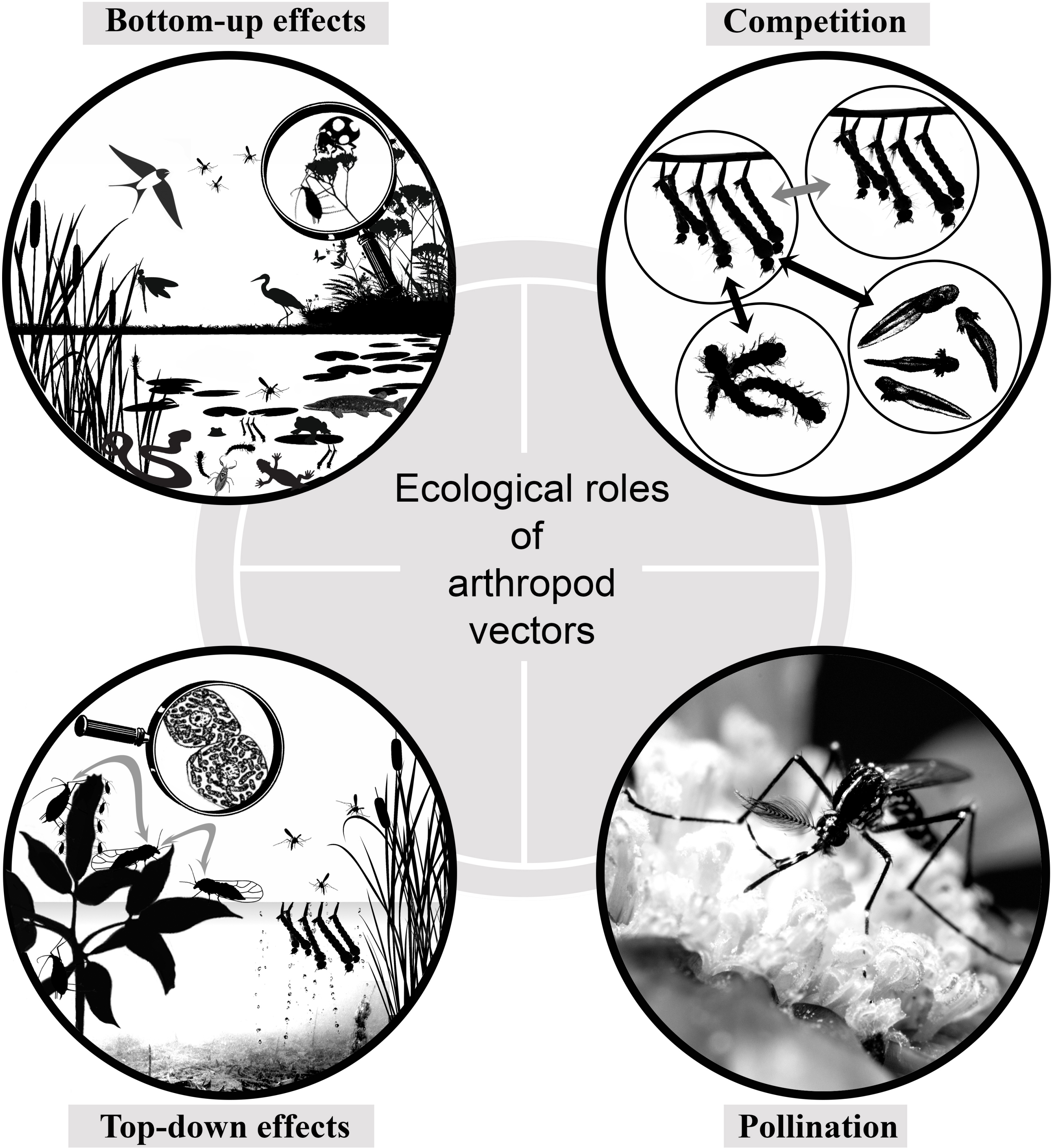


Figure 1


Bottom-up effects
Competition
Ecological roles of arthropod vectors
Top-down effects
Pollination

Culex_pipiens_female_felicia_amelloides

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Culex_pipiens_male_felicia_amelloides

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Culex_pipiens_female_aphid_erigeron

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Culex_pipiens_male_aphid_erigeron

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Culex_pipiens_male_brassica

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