

Seasonal insect migrations: massive, influential, and overlooked

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During seasonal changes around the globe, trillions of insects are on the move. Many insect populations, including butterflies, moths, hoverflies, and dragonflies, make repeated seasonal migrations each year. It is only during the past century that biologists have come to accept the concept of insect migration, and new research using radar, citizen science, and stable isotopes has revealed unexpected insights about this phenomenon. Drawing on these findings, we demonstrate how seasonal insect movements are both massive and ecologically influential, with consequences for food webs, nutrient transport, pollination, and infectious disease. Responding to environmental changes, some mobile insect populations are declining or shifting the timing and extent of their journeys. We suggest research and policy priorities for investigating and protecting insect migrations. Outcomes from such work could transform strategies for agricultural pest control and wildlife conservation, and could help preserve the ecological functions performed by migratory insects.

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Every year around the globe, insects undertake massive seasonal movements at a far greater scale than was previously recognized. Research on migratory animals has primarily focused on vertebrates (Dingle 2014), but recent findings demonstrate that most terrestrial migrants are insects, surpassing vertebrates in both abundance and biomass (Holland *et al.*

2006; Chapman *et al.* 2015). One radar study revealed that 2–5 trillion high-flying insects make long-range seasonal movements annually above the southern UK alone (Hu *et al.* 2016). These migrations are ecologically distinct from those of vertebrates, often making use of seasonal winds and requiring multiple generations to complete a full cycle, due to short insect life spans (Figure 1; Chapman *et al.* 2011). Seasonal migrations of insects vary widely in their spatial patterns (Figure 2; Panel 1), encompassing both the classic round-trip migrations of numerous hoverfly, dragonfly, and butterfly populations (such as monarch butterflies [*Danaus plexippus*] and painted ladies [*Vanessa cardui*]) as well as the more complex movements of desert locusts (*Schistocerca gregaria*) and Australian armyworm moths (*Mythimna convecta*), whose migratory journeys form interconnected networks across continents. Other insects like mustard aphids (*Lipaphis erysimi*) and green lacewings (*Chrysoperla carnea*) demonstrate seasonal migrations radiating out from source sites, resulting in repeated population-scale patterns (Drake and Gatehouse 1995). Here, we define insect migrations broadly to include seasonal movements of insect populations that involve large numbers of individuals and repeat in terms of time (annually or otherwise), space (over the same geographic area), and direction.

Insect migrations influence ecosystem function and human life (Figure 3). Insects in general are critical to ecological processes; they decompose organic matter, regulate pests, pollinate crops, and represent important sources of food for many vertebrates (Losey and Vaughan 2006). Migratory insects in particular affect ecological interactions by connecting distant ecosystems, transporting nutrients and propagules (eg pollen) over long distances, and structuring food webs (Bauer and Hoyer 2014). As one example, two billion Bogong moths (*Agrotis infusa*) migrate up to 1000 km each spring into the Australian Alps to aestivate in caves, where they deposit 7.2

In a nutshell:

- The seasonal migrations of insects link much of the natural world in ways not previously recognized
- Globally, most terrestrial animal migrants are insects; massive numbers of moths, butterflies, and other insects undertake seasonal population-level movements that repeat periodically and often traverse vast distances
- Migratory insects transport pollen, pathogens, energy, and nutrients
- Evidence suggests that mobile insects in terrestrial systems are ecologically important for food webs, agriculture, ecosystems, and human health, with cumulative effects analogous to those of plankton in oceans
- As some migratory insect populations decline or alter their journeys amid environmental changes, science-based policy and research are needed to conserve insect migrations

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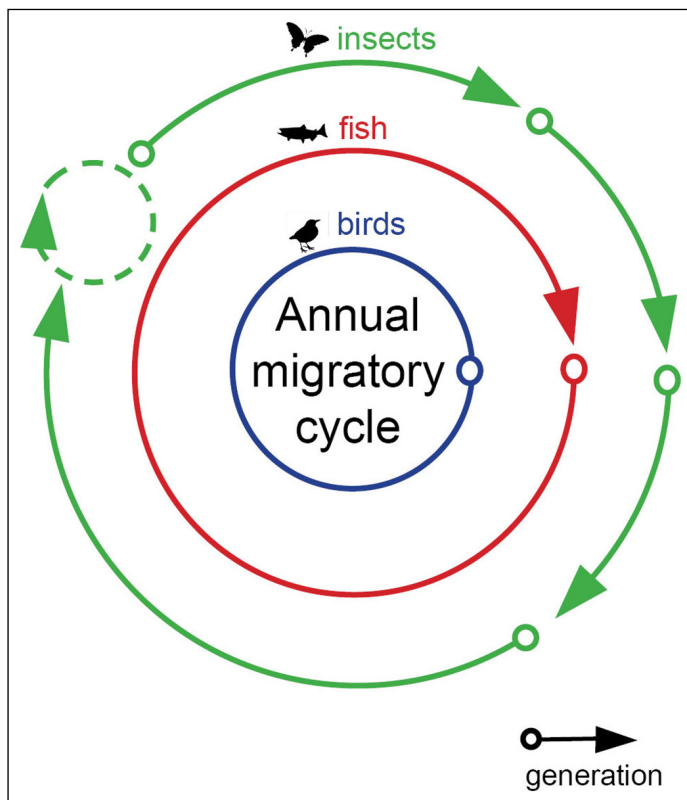


Figure 1. Taxonomic groups of migratory animals exhibit different generational and spatiotemporal patterns in their annual cycles. Individual birds (as well as mammals, not shown) typically repeat numerous migrations throughout their lives; fish often complete migration within one generation (dying after 1–2 full cycles); and migratory insects frequently require multiple generations to complete a single annual cycle. As such, insect migrations often play out like relay races, with different generations completing each leg of the journey. Some insect generations advance the migration (solid arrows), whereas other generations move shorter distances or behave as residents (dashed arrow).

metric tons of nitrogen (N) per year (Green 2011) and serve as a primary food source for the critically endangered mountain pygmy possum (*Burramys parvus*).

Scientific understanding of insect migration lags behind that of vertebrate migration (Chapman *et al.* 2015). This is partly because the small size of insects precludes the use of most individual-based devices, typically designed to track vertebrates (Chapman *et al.* 2011), but also because the existence of long-distance insect migrations was not fully accepted by biologists until the 1900s (Panel 1; Williams 1958). New approaches are revealing the nature of insect migrations but alongside these discoveries is growing evidence of severe declines in insect populations (Dirzo *et al.* 2014; Sánchez-Bayo and Wyckhuys 2019). For example, flying insect biomass in Germany has been reduced by 76% over the past 30 years (Hallmann *et al.* 2017). These declines lend urgency to the need for greater understanding of how seasonal insect migrations will respond to environmental change.

We propose that migratory insects in the aerosphere represent such tremendous biomass and play such crucial roles in

ecosystems that their ecological impacts are akin to that of plankton in the ocean; indeed, early investigators called them “aerial plankton” (Johnson 1969). We synthesize evidence showing that (1) insects participate in mass seasonal migrations in far greater abundance and with greater diversity than previously recognized; (2) insect migrants act as mobile links, transporting energy, nutrients, pollen, and pathogens across ecosystems (Figure 4); and (3) amid rapid environmental change, many insect migrations could shift or disappear before they are fully understood. We highlight future research questions and suggest that insect migrations merit urgent scientific investigation with the same rigor and effort applied to vertebrate migrations. Outcomes from such research will inform agricultural pest control, wildlife conservation, and community ecology.

Scale and scope of seasonal insect migrations

Aggregations of migratory insects caught the attention of naturalists well over a century ago (Williams 1958). For instance, monarch butterflies were reported to be moving in large numbers through Maryland in 1886, with “the whole heavens swarming with butterflies” reaching “beyond the range of vision” (Ellzey 1889). Only recently has technology such as vertical-looking entomological radar allowed scientists to quantify insects beyond the range of human perception; this work has revealed that low-altitude insect movements, while spectacular, pale in comparison to inconspicuous movements at higher altitudes (150–1200 m; Chapman *et al.* 2011). Radar and citizen-science data on painted lady butterflies in the UK, for example, indicated that high-altitude migrations were much larger than previously assumed. Approximately seven million painted ladies arrived in the UK from southern Europe during spring 2009, and 14 million returned southward during fall, completing a 15,000-km annual migration requiring six generations (Stefanescu *et al.* 2013). Silver Y moths (*Autographa gamma*) migrate in even greater numbers, with up to 700 million departing from the UK in the fall (Chapman *et al.* 2012). Although these studies suggest that migratory insect numbers are vast (Holland *et al.* 2006), this was verified on an even grander scale when researchers documented massive insect “bioflows” of numerous species over the south-central UK. Entomological radar and aerial netting data detected annual movements involving trillions of insects, with an estimated biomass greater than 2000–5000 metric tons, over a 70,000-km² area, exceeding by sevenfold the biomass of songbird migrants departing the UK each fall (Hu *et al.* 2016).

Insects making seasonal journeys are diverse in terms of numbers of species and taxonomic breadth (Figures 5 and 6; Chapman *et al.* 2015). Hundreds of insect species are known to migrate (WebTable 1), a behavior that has evolved separately multiple times (Dingle 2014) across at least ten taxonomic orders. Yet the scope of seasonal insect migration likely

Panel 1. Historical context and definitions of insect migration

The concept of seasonal insect migration was initially met with skepticism. Although early records note massive insect swarms – locusts in the Book of Exodus, for instance – and directional movements, scientists in the early 1900s remained doubtful that insects could move more than a few kilometers (Williams 1958; Sorensen 1995). Research, particularly at the Rothamsted Experimental Station in the UK (Taylor 1986) and in the American South (Glick 1939; Johnson 1969), changed this perception. Early volunteer networks also made discoveries about monarch butterflies (*Danaus plexippus*) and moths in the UK (using tags and light traps) in the 1950s, by which time long-distance insect movement was more widely accepted (Taylor 1986). However, the belief that insect movements were strictly passive persisted into the 1980s and beyond, with migrants presumed to be blown haphazardly by the winds (Rabb and Stinner 1979). In recent decades, the use of radar has illuminated notable findings, demonstrating that some large-bodied insects sense and selectively choose high-altitude winds in which to fly, collectively creating dense, fast “bioflows” of diverse insects moving in favorable directions and reversing seasonally (Chapman *et al.* 2011, 2015). Evolutionary drivers of insect migrations are also better understood (Chapman *et al.* 2015); these drivers include the need for

insects to escape unfavorable conditions, to exploit distant and seasonal resources (Chapman *et al.* 2012), and to spread offspring over variable landscapes (Holland *et al.* 2006).

Entomologists now recognize that migratory insects display diverse movement trajectories (Figure 2), including round-trip migrations, complex interconnected movement networks with fusing and branching subpopulation pathways, and movements that appear unidirectional (though often have inconspicuous return routes; Drake and Gatehouse 1995). Some entomologists and migration biologists recognize all of these as migrations, so long as they meet a set of behavioral criteria observed at the individual level (Dingle 2014; Chapman *et al.* 2015), whereas others (especially vertebrate biologists) describe only round-trip (“to-and-fro”) movements as true migrations. We define insect migration broadly and at the population scale (rather than for individuals) for our purposes, examining the ecological effects of collective movements with a predictable direction that coincide with seasonal changes and repeat over time. For insects, these movements can involve multiple generations (seen most commonly) or a single generation (eg Bogong moths [*Agrotis infusa*] for a full annual cycle, and may be self-propelled, wind-propelled, or both (Chapman *et al.* 2015).

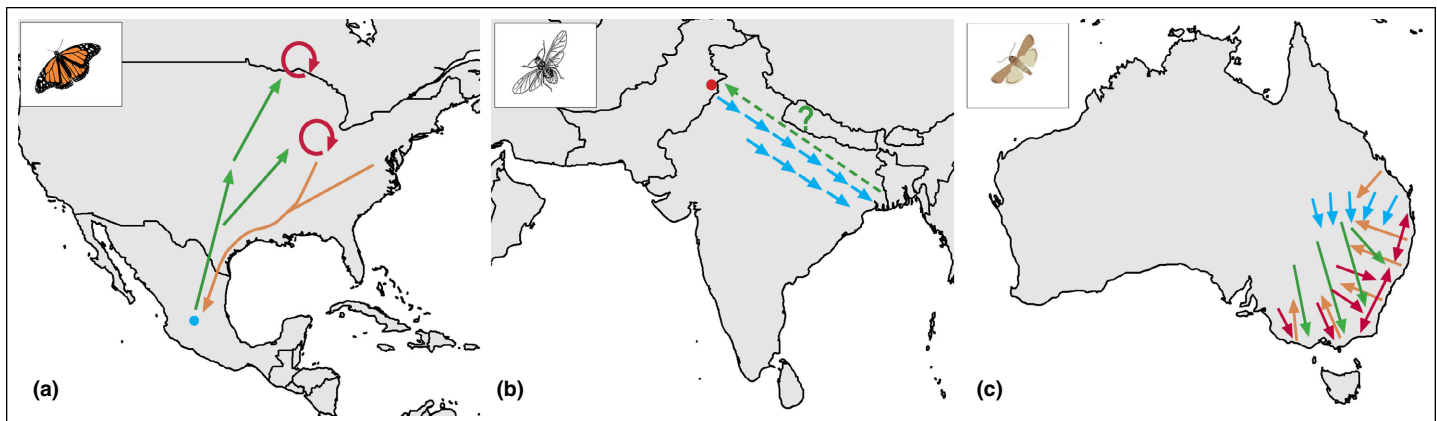


Figure 2. Insect populations undertake seasonal movements with a diverse range of complex population trajectories. Examples here show simplified generational and subpopulation movements (arrows) or hibernacula locations (solid circles) throughout an annual cycle, during fall (orange), winter (blue), spring (green), and summer (red), for: (a) round-trip migrations of monarch butterflies (*Danaus plexippus*) in eastern North America; (b) repeating winter movements of mustard aphids (*Lipaphis erysimi*) from the west Himalayan Hills region to the plains of northeastern India, with westward return movements unclear (adapted from Ghosh *et al.* [2019] under CC BY 4.0 [creativecommons.org/licenses/by/4.0]); and (c) complex interconnecting networks of Australian armyworm moths (*Mythimna convecta*), which have overlapping population and generation pathways, yet generally show repeated directional movements (adapted from Drake and Gatehouse [1995]).

remains vastly underestimated (Hu *et al.* 2016). Many journeys have been described only in the past decade. For example, the migration of wandering glider dragonflies (*Pantala flavescens*) over the Indian Ocean – the longest-known insect migration, potentially totaling 17,000 km – was first documented in 2009 (Anderson 2009). We hypothesize that thousands of insect species undertake seasonal migrations annually and that the number of individual insects involved may be as high as 1×10^{15} – 10^{16} globally, a figure roughly equal to the estimated total

number of ants in the world at any given time (Holldobler and Wilson 2008).

Networks of radar and other monitoring technologies are needed to better characterize the spatiotemporal patterns of insect migrations. The European Network for the Radar surveillance of Animal Movement (ENRAM) enables aerial investigation of bats, birds, and insects (Bauer *et al.* 2017); similar research is needed on other continents. Identifying migratory insect species and characterizing movement path-

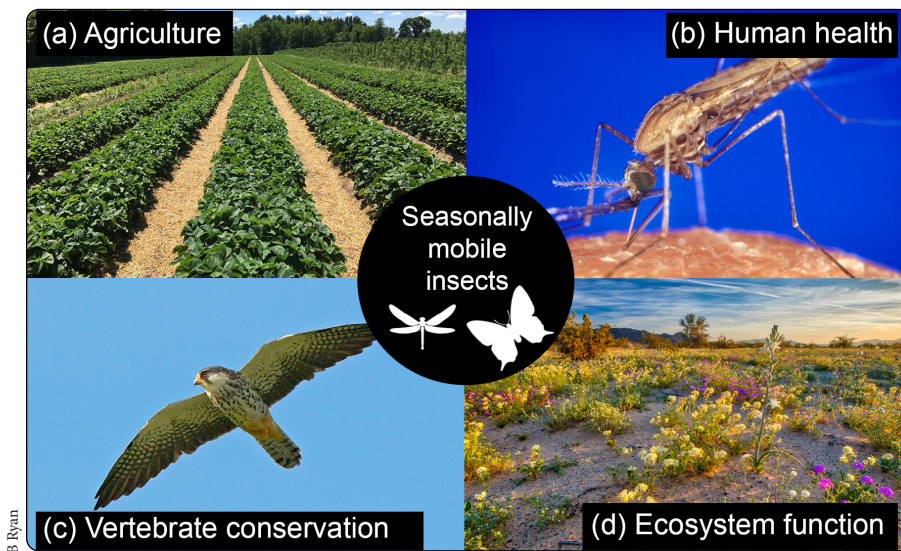


Figure 3. Insect populations that make repeated seasonal movements can affect (a) *agriculture*, with migratory insects acting as crop pests (eg diamondback moths [*Plutella xylostella*] causing more than US\$1 billion in damages annually) as well as agents of pest control (eg migratory hoverflies, which consume 1 million aphids per hectare of cropland in the southern UK; Wotton *et al.* [2019]); (b) *human health*, with recent evidence suggesting (as one example) that seasonal movements of *Anopheles* spp mosquitoes could explain the persistence of malaria in some parts of the African Sahel (Huestis *et al.* 2019); (c) *vertebrate conservation*, with many birds, bats, and other animals feeding on migratory insects for part of the year; for example, Amur falcons (*Falco amurensis*) may consume wandering glider dragonflies during the dragonflies' seasonal migration across the Indian Ocean (Anderson 2009; Chapman *et al.* 2015); and (d) *ecosystem function*, with migratory insects affecting nutrient transport (eg Bogong moths [*Agrotis infusa*] moving nitrogen), pollen transport, and other processes.

ways will require the development of increasingly small tracking devices, ones that weigh <0.1g (Kissling *et al.* 2014). For phytophagous insects, analysis of host plant secondary compounds in insect tissues can help to pinpoint the natal origins of migrants (eg as was done with cardenolides, a type of steroidal toxin found in monarch butterfly tissue, derived from different milkweeds; Satterfield *et al.* [2018]). Likewise, naturally occurring stable isotopes in insect tissues act as especially powerful tools for delineating insect migrations and their multigenerational structure. For example, stable isotopes confirmed the southward migration of true armyworm moths (*Mythimna unipuncta*) from the northern US through Texas (Hobson *et al.* 2018). Multiple studies have used stable hydrogen and carbon isotopes to examine the migratory patterns of North American monarch butterflies. One such study showed that the natal origins of migratory monarchs sampled in Mexico varied over four decades according to annual climatic factors affecting larval development and host plant condition (Flockhart *et al.* 2017). These investigations contribute to our understanding of full annual cycle biology, which has illustrated how different spatiotemporal phases of a migratory population's annual cycle are inextricably linked. The need for such full annual cycle studies has been clearly stated for vertebrates, and we expand this call to include research on insects (Marra *et al.* 2015).

Ecological implications of insect migrations

Migratory insects play many distinct ecological roles. Animal migrants of any taxa provide ecosystem services by connecting geographically distant habitats (Altizer *et al.* 2011; Lopez-Hoffman *et al.* 2013; Bauer and Hoyer 2014). Migrants act as “resource linkers” when transporting organic matter, as “genetic linkers” when carrying pollen and other propagules, and as “process linkers” through trophic interactions that structure food webs and biodiversity patterns (Lundberg and Moberg 2003; Jeltsch *et al.* 2013). Migratory vertebrates have already been recognized in these processes. In contrast, the role of migratory insects has been undervalued (Bauer and Hoyer 2014; Hu *et al.* 2016) but could be especially influential due to the sheer scale of their movements and their characteristic biological features.

Nutrient transfer

Just as Pacific salmon (*Oncorhynchus* spp) transfer nutrients from ocean to forest ecosystems (Dingle 2014), migratory insects – when experiencing mortality along annual routes – transport N and phosphorus (P) to distant ecosystems through carcass deposition. The multi-generational nature of seasonal insect movements could provide frequent opportunities for nutrient deposition, with generations expiring at various points along the annual route. Moreover, insect migrations that involve massive movements in one direction but less pronounced return movements later in the year could facilitate annual latitudinal shifts in nutrients. A handful of case studies demonstrate migrant insects' capacity for nutrient transport. Hoverflies making long-range seasonal migrations to and from northern Europe transport 1000–2500 kg of N and 100–250 kg of P per year over a 300-km-wide area in the UK (Wotton *et al.* 2019). Bogong moths in the Australian Alps contribute 7249 kg of N and 969 kg of P per year, a level of nutrient influx similar to that provided by salmon in Alaska's Kachashan River (Green 2011). Desert locusts travel up to 5000 km in complex migratory networks in northern Africa, where they can number 50 million per square kilometer, representing 2350 kg of N and 225 kg of P (Landry and Parrott 2016). Summed across species, the insect community flying over the southern UK represents 100,000 kg of N and 10,000 kg of P (equating to 0.2% and 0.6–4.7% of the region's total atmospheric depositions of N and P, respectively), figures that underscore the importance of insect movement in nutrient transport (Hu *et al.* 2016).

Pollen dispersal and gene flow

Migratory insects could successfully disperse pollen over long distances, provided that individuals revisit the same flowering species and that pollen remains viable en route. Numerous studies demonstrate long-distance pollen transport by migratory noctuid moths (WebTable 2) and hoverflies (Wotton *et al.* 2019). For instance, 30% of Australian bollworm (*Helicoverpa punctigera*) and 18% of cotton bollworm (*Helicoverpa armigera*) moths in Australia carried pollen that originated ~500–1500 km away (Gregg 1993). Pollen carried by *H. armigera* remains viable for only 1–2 days (Richards *et al.* 2005), but moths can travel hundreds of kilometers per night (Chapman *et al.* 2011).

If mobile insects achieve long-distance pollination, then we would expect a higher degree of genetic diversity and a lower degree of population genetic structure in those plants across their ranges. Studies provide some evidence but remain limited. Among *Pithecellobium elegans* canopy trees in Costa Rica, 29% of fertilizations involved pollen from outside the population, potentially due to pollination by migratory hawkmoths (Chase *et al.* 1996). Although studies of insect-mediated gene flow at larger spatial scales are scant, fig wasps (*Ceratosolen arabicus*) making seasonal movements on easterly winds in Africa have been shown to transport the pollen of fig trees (*Ficus sycomorus*) up to 160 km. The wasps' long-distance journeys allow pollen to move easily even between trees that are far apart, creating a panmictic fig tree population (ie showing little genetic differentiation) along a 250-km stretch of the Ugab River in Namibia (Ahmed *et al.* 2009). In Spain, fragmented populations of endangered violets (*Viola cazorlensis*) showed unexpectedly high gene flow, which researchers attributed to long-distance migrations of the plant's only known pollinator, the hummingbird hawkmoth (*Macroglossum stellatarum*; Herrera and Bazaga 2008). Future research could investigate the degree to which migratory insects provide directional, periodic waves of pollination (eg southward in fall; Wotton *et al.* 2019) through signals reflected in plant population genetic structure.

Pathogen dynamics

Insect movement is frequently recognized as a primary driver of the spread of crop diseases, and here we suggest that seasonal insect migrations may also influence animal pathogens, including those affecting humans and other insects. Insect migrants have rarely been investigated for involvement in the spread of human pathogens, in part because most vectors were assumed to be incapable of regular long-distance movements (Sellers 1980). However, new evidence of insect movement and rising concerns about vector-borne diseases now make this a research priority. Black flies (*Simulium damnosum* complex) that transmit the nematode that causes river blindness (*Onchocerca volvulus*) travel hundreds of kilometers in a southwesterly direction annually on monsoon winds over West Africa,

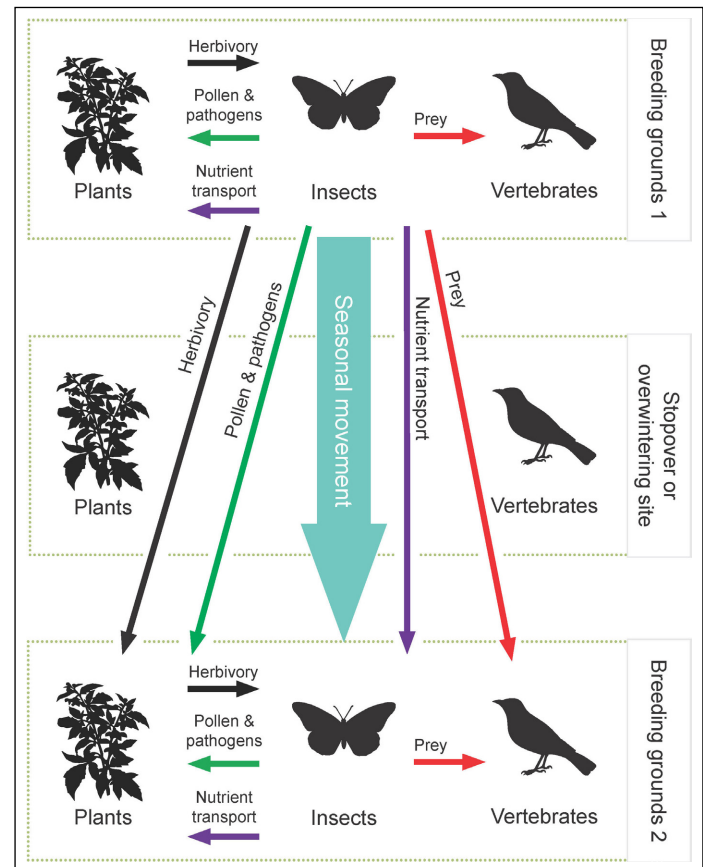


Figure 4. Whereas resident insects influence ecological processes within local breeding or wintering grounds, seasonally migratory insects can affect ecological processes across vastly distant and distinct ecosystems (eg at breeding grounds, wintering sites, stopover locations). Interactions across ecosystems include herbivory, predation, pollination, pathogen transport, and nutrient transfer. In addition, mobile insects contribute to indirect effects (not pictured) across ecosystems as well as across trophic levels, such as when predator consumption of mobile insects in one ecosystem affects other predators or plants in a distant ecosystem.

facilitating the parasite's rapid spread. Management strategies that take vector movement into account have helped to prevent new cases of river blindness (Reynolds *et al.* 2006). Recent compelling evidence suggests that other vectors, including some *Anopheles* and *Culex* mosquitoes, undertake high-altitude seasonal migrations while carrying deadly pathogens (assisted by seasonally predictable winds), which could explain the annual re-occurrence of diseases like Japanese encephalitis and malaria (Reynolds *et al.* 2006; Dao *et al.* 2014; Huestis *et al.* 2019). Although long-distance pathogen transport by arthropod vectors remains controversial, this topic merits further investigation.

Pathogens that cause disease in insects themselves are also profoundly affected by host seasonal movements. In general, animal migrations (across taxa) can in some cases disperse pathogens over long distances and contribute to their spatial spread. In other cases, long-distance migrations reduce animal infection risk (Altizer *et al.* 2011), particu-



Figure 5. Migratory insects are diverse, occurring in at least ten taxonomic orders. Here, we note example species from five orders within the Endopterygota superorder: (a) Lepidoptera (striped hawkmoth [*Hyles livornica*]); (b) Diptera (marmalade hoverfly [*Episyrphus balteatus*]); (c) Coleoptera (seven-spotted lady beetle [*Coccinella septempunctata*]); (d) Neuroptera (common green lacewing [*Chrysoperla carnea* complex]); and (not pictured) Hymenoptera (African honeybee [*Apis mellifera scutellata*]). For more details, see WebTable 1.

larly if infected hosts are removed from the population during strenuous journeys (“migratory culling”) or if migrants temporarily escape parasite-contaminated habitats (“migratory escape”). Both mechanisms have been demonstrated in migratory insects, including fall armyworm moths (*Spodoptera frugiperda*) infected by nematodes and monarchs affected by protozoa (Altizer *et al.* 2011). Investigating infection dynamics in other mobile insects, which are conducive to large-scale experiments and field monitoring, could elucidate how host movement and infectious diseases interact, and may help to support predictions of how insect pathogens will respond to global change.

Food web interactions

Insects serve as prey for many vertebrates (and invertebrates, which are not addressed here). More than two-thirds of the world’s bat species are insectivores (Kunz *et al.* 2011), and 89% of bird species in the US depend partially or entirely on insects, especially during the breeding season (Losey and

Vaughan 2006). Migratory insects could therefore offer prey pulses for insectivorous birds, mammals, and other predators (WebPanel 1; WebFigure 1), with consequences for predator populations. Such resource pulses can bolster predator growth rates during critical periods and periodically decouple local predator–prey dynamics. One example of this occurs through prey-switching (Terry *et al.* 2017), such as when local predators temporarily forego local prey to feed on mass arrivals of migratory insects (eg black kites [*Milvus migrans*] and desert locusts; WebPanel 1; WebFigure 1), creating a “trophic interaction modification” (when a consumer–resource interaction is modified by a third species; Terry *et al.* 2017). Resident prey could initially experience reduced mortality, and trophic cascades could result if (for example) local herbivores consume more plant biomass due to temporary release from predation. By mediating interactions between resident animals, migratory insects could alter species coexistence and food web stability, a subject that is also in need of further research (Lundberg and Moberg 2003; Jeltsch *et al.* 2013; Bauer and Hoyer 2014). Field studies that quantify



Figure 6. In addition to five orders from the Endopterygota superorder, migratory insects also occur among five orders within the Exopterygota superorder, including (a) Odonata (green darner [*Anax junius*]); (b) Hemiptera (large milkweed bug [*Oncopeltus fasciatus*]); (c) Orthoptera (desert locust [*Schistocerca gregaria*]); (d) Thysanoptera (soybean thrips [*Neohydatothrips variabilis*]); and (not pictured) Ephemeroptera (*Ephemerella maculata*). For more details, see WebTable 1.

shifts in predator diets before, during, and after the arrival of mobile insects (eg Krauel *et al.* 2017) could be paired with dynamic predator–prey models to identify mechanisms by which insect movements disrupt local food webs.

In addition to having direct effects, migratory insects could have indirect effects across distant ecological communities and trophic levels (Figure 4). For instance, black-backed orioles (*Icterus abeillei*) and black-headed grosbeaks (*Pheucticus melanocephalus*) consume an average of 15,067 monarch butterflies per day at monarch overwintering colonies in Mexico, killing an estimated 7–44% of monarchs per colony (Brower and Calvert 1985). We suggest that such predation could reduce the number of monarchs available to later recolonize northern breeding grounds and, in effect, shrink resource pulses for natural enemies in distant ecosystems. This could also limit monarch herbivory on host plants in northern areas through density-dependent effects. As such, predators in one ecological community could indirectly influence natural enemies and plants in other, vastly distant communities – via their impacts on migratory insect prey. We speculate that migratory insects create indirect links across ecosystems that are not oth-

erwise connected, a mechanism attributable to the insects' mobility and central placement in food webs as herbivores, predators, and prey (Thompson 1984).

■ Responses to environmental change

As scientific knowledge about the ecological importance of insect movement expands, so too does awareness of the precipitous decline of many insect species and populations around the globe (Sánchez-Bayo and Wyckhuys 2019). The abundance of moths and butterflies, viewed as indicators of biodiversity health and representing numerous migratory species, has declined by 35% globally over the past 40 years (Dirzo *et al.* 2014). A mounting number of studies corroborate this trend in Europe (eg Powney *et al.* 2019) and North America (eg Forister *et al.* 2011). These patterns raise questions about whether seasonal insect migrations will shift or disappear before they are documented.

Many insects are altering the timing or geographic extent of their seasonal movements in response to environmental change. Some migrants have already shifted their ranges

poleward due to climate change (eg oleander hawkmoths [*Daphnis nerii*] in Japan; Ohba *et al.* 1999), and warmer temperatures are increasing the frequency of migrant lepidopteran species at more northern latitudes (Sparks *et al.* 2005). Records of changes in migratory timing abound in the literature. Bogong moths now arrive a full month earlier at aestivation sites than they did in the 1950s (Caley and Welvaert 2018), and peach-potato aphids (*Myzus persicae*) complete seasonal movements 16 days earlier for each 1°C increase during winter (Harrington and Woiwod 2007). A few insect subpopulations, including North American monarchs in parts of the southern US (Satterfield *et al.* 2018), have shifted from migratory to non-migratory behaviors in response to human-provided food plants, which enable monarchs to forego migration and reside in the same locations year-round. Warmer winters may hasten such changes, with residency predicted to increase for other migratory lepidopterans (Sparks *et al.* 2005).

In addition to spatiotemporal shifts, some migratory insect populations are in decline. North American monarch colonies in Mexico fell by >80% between 1993 and 2017 (Thogmartin *et al.* 2017). Other declining migratory insects include cloudless sulphur (*Phoebis sennae*) and question mark (*Polygonia interrogationis*) butterflies in the US (Breed *et al.* 2013) and giant honeybees (*Apis dorsata*) in India (Sihag 2014). The case of the Rocky Mountain locust (*Melanoplus spretus*) demonstrates that even the most abundant mobile insects are vulnerable to extinction. These locusts once made dry-season movements in plague-like numbers from high-altitude to low-altitude zones in the Rocky Mountains, but by 1904 had mysteriously disappeared (Sorensen 1995). Recent trends call for vigilance to prevent future species losses. Some widespread macro-moths (even pests) are decreasing in the UK, including migratory silver Y, black cutworm (*Agrotis ipsilon*), and turnip (*Agrotis segetum*) moths (Conrad *et al.* 2006).

There is a critical need to monitor migratory insects' range shifts and declines, which are already occurring, and to document ecological consequences. One useful analysis (eg using weather radar or long-term citizen-science monitoring) could examine how migrant insects are faring in comparison to resident insects in the same taxonomic order. Several studies suggest that some mobile lepidopterans are declining less severely than residents; other migrant insects remain stable (Conrad *et al.* 2006; Forister *et al.* 2011). In cases where migratory insects are more resilient than residents, migrants could help to maintain ecosystem services and sustain imperiled vertebrate populations amid environmental changes.

■ Conclusions and policy gaps

If insects are “the little things that run the world” (Wilson 1987), then it is crucial to investigate and protect their massive seasonal migrations. Research on the full annual cycle biology of migratory insects is urgently needed to

(1) quantify their abundance and diversity, (2) estimate nutrient transport, (3) investigate effects on the phenology of species interactions, and (4) examine responses to anthropogenic environmental changes. A combination of radar, citizen science, field investigations, and molecular assays, coupled with smaller tracking technology, will enable this work.

Land management practices in terrestrial systems should recognize and support the *full* community of migratory animals, including birds, mammals, and insects. Restoring landscapes with native plants could provide resources for a diversity of migrants; for insects, this would supply nectar and food sources to fuel migrants' journeys. Efforts to revive insect flyways and habitats could include incentivizing the planting of native species for businesses and landowners, promoting large-scale habitat restorations on public lands, and shifting mowing schedules.

Some migratory insects will require new legislative protections, as gaps in conservation policy leave insects vulnerable. Animal migrants of any taxonomic group are challenging to protect and require coordinated conservation efforts across international borders. The US Endangered Species Act (ESA) of 1973 has helped some migratory species recover but typically functions for only extremely imperiled populations and fails as a mechanism to preserve migration as a “phenomenon of abundance” (Fischman and Hyman 2010). Even when migrants do receive special protections, insects are rarely considered. The Convention on the Conservation of Migratory Species of Wild Animals (CMS) currently protects 650 vertebrate species and only one insect species. To date, the ESA lists 89 insect species, compared to 1097 vertebrate species (FWS 2019), grossly disproportionate to the number of described taxa per group. Contributing to this problem are restrictions on which types of insects can be listed, the dependence of many insects on narrow habitat ranges, and severe data deficiencies (Dunn 2005).

We suggest that preserving the world's animal migrations cannot be achieved without policies that specifically protect insects, which engage in spectacular and ecologically important journeys and account for the majority of terrestrial migrants. As opposed to current efforts to diminish protections under the ESA, policy affecting insects must be strengthened and restrictions lifted to allow the listing of distinct populations (rather than only species or subspecies, to which invertebrates are currently limited). We likewise recommend that Parties of the CMS assess migratory insects for Appendix listing and establish national legislation with specific protections for insects. National strategies for pollinator and insect conservation are needed to implement native plant restoration projects at the landscape scale, preserve movement corridors and breeding habitats, and support the large population sizes required to sustain ecologically viable migrations (Fischman and Hyman 2010). The influence of mobile insects on agriculture, conservation, human health, and ecosystem function suggests an urgent need for protections of insect migrations in the next decade to prevent further losses of this phenomenon.

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