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Essay

The insect apocalypse, and why it matters

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The majority of conservation efforts and public attention are focused on large, charismatic mammals and birds such as tigers, pandas and penguins, yet the bulk of animal life, whether measured by biomass, numerical abundance or numbers of species, consists of invertebrates such as insects. Arguably, these innumerable little creatures are far more important for the functioning of ecosystems than their furry or feathered brethren, but until recently we had few long-term data on their population trends. Recent studies from Germany and Puerto Rico suggest that insects may be in a state of catastrophic population collapse: the German data describe a 76% decline in biomass over 26 years, while the Puerto Rican study estimates a decline of between 75% and 98% over 35 years. Corroborative evidence, for example from butterflies in Europe and California (which both show slightly less dramatic reductions in abundance), suggest that these declines are not isolated. The causes are much debated, but almost certainly include habitat loss, chronic exposure to pesticides, and climate change. The consequences are clear; insects are integral to every terrestrial food web, being food for numerous birds, bats, reptiles, amphibians and fish, and performing vital roles such as pollination, pest control and nutrient recycling. Terrestrial and freshwater ecosystems will collapse without insects. These studies are a warning that we may have failed to appreciate the full scale and pace of environmental degradation caused by human activities in the Anthropocene.

A key feature of the Anthropocene is the accelerating decline of biodiversity. Public perception of this loss is particularly focused on extinction events, especially those of large mammals such as the northern white rhino or birds such as the passenger pigeon or dodo. Sad though these events are, the actual proportion of species that have so far gone extinct during the modern era are relatively small. Just 80 species of mammal and 182 species of bird have been lost since 1500, representing 1.5% and 1.8%, respectively, of the known species [1] (note that this time period excludes the wave of extinctions that took place in the late Pleistocene when man first spread around the world). On the face of it, these figures would seem to be at odds with the notions that we are in the midst of the ‘sixth mass extinction event’, or that biodiversity is in crisis. However, evidence has recently begun to emerge suggesting that global wildlife has been affected far more profoundly than these relatively modest figures for actual extinctions might suggest.

Most species may not yet have gone extinct, but they are, on average, far less abundant than they once were. A recent landmark paper by Bar-On *et al*. [2] estimated that 83% of wild mammal biomass has been lost since the rise of human civilization. The scale of human impact is also revealed by their estimate that wild mammals now comprise just 4% of mammalian biomass, with livestock comprising 60% and humans the remaining 36%. They also calculate that 70% of global avian biomass is made up of domestic poultry. Also released in 2018 was the World Wildlife Funds and Zoological Society of London’s ‘Living Planet Report’ [3], which estimates that the abundance of the world’s wild vertebrates (fish, amphibians, reptiles, mammals and birds) fell by 60% between 1970 and 2014. I was born in 1965, and in my lifetime we have moved from an age of bio-abundance to one of bio-paucity. One has to wonder what wildlife will be left by the time my teenage children reach my age.

Catastrophic though declines of wild vertebrates have been, it seems that another even more dramatic change may have been quietly taking place, one that may have more profound implications for human wellbeing. The large majority of known species are invertebrates, dominated

Figure 1. Food for nearly all.
Insects are at the heart of food webs, being consumed for example by birds, bats, small mammals, reptiles, amphibians, spiders, and other insects. Here a green bee-eater, *Merops orientalis,* feeds on a butterfly (credit: Dr. Raju Kasambe [CC BY-SA 4.0], from Wikimedia Commons).

on land by the insects. Insects are far less well studied than vertebrates, and for the majority of the one million species that have so far been named we know essentially nothing about their biology, distribution or abundance. There are estimated to be at least another 4 million species that we have yet to discover [4]. In 2017, a paper was published by the Krefeld Society, a group of entomologists who had been trapping flying insects in Malaise traps on nature reserves scattered across Germany since the late 1980s [5]. It was the only long-term dataset in existence which encompasses a broad suite of insect species. The study found that the overall biomass of insects caught in their traps fell by 75% in the 26 year period from 1989 to 2014. In midsummer, the peak of insect activity, the decline was even more marked, at 82%. That we could have lost such a large proportion of insect biomass in such a short period of time was scarcely credible. Bear in mind also that the impacts of mankind on the planet were at play long before 1989, so it seems probable that this 75% drop is just the tail end of a much larger fall. We will never know how many insects there were, say, 100 years ago, before the advent of pesticides and industrial farming.

There has been much debate as to whether similar declines in insect abundance are occurring elsewhere, but hard data are largely lacking. Only butterflies and moths have been monitored extensively, in various localities from California to Europe from 1970 onwards, and they show pervasive patterns of decline, though rarely as dramatic in magnitude as the German data [6–8]. The most high profile example is the eastern North American population of the monarch butterfly (*Danaus plexippus*), famed for its long migration to and from overwintering sites in Mexico, populations of which fell by 80% in the ten years to 2016 [9].

Indirect evidence in support of the notion that there have been large declines in insect abundance come from declines of insectivorous birds in North America and Europe. For example aerial insectivorous birds have declined more than any other bird taxon in North America, by about 40% between 1966 and 2013 [10]. In the UK, populations of the spotted flycatcher, *Muscicapa striata*, fell by 93% between 1967 and 2016 [11]. Other once-common insectivores have suffered similarly, including the grey partridge (*Perdix perdix*; -92%), nightingale (*Luscinia megarhynchos*; -93%) and cuckoo (*Cuculus canorus*; -77%) [11].

All of the evidence above relates to insect populations in highly industrialized, developed countries. In 2018, Lister and Garcia [12] published what is, arguably, the most concerning data set on this subject so far. In 1976 and 1977 Lister sampled arthropod abundance in rainforest using sweep nets and sticky traps. Returning to the same sites 35 years later, Lister and Garcia repeated the sampling between 2011 and 2013. They found that the biomass of insects and spiders in sweep net samples had fallen between 75 and 88%, depending on the time of year. Sticky trap sample catches had fallen by 97 to 98%. The most extreme comparison was comparing identical sticky traps placed out in January 1977 versus January 2013, with the catch declining from 470 mg of arthropods per day to just 8 mg.

Although the long-term data on insect populations are spectacularly inadequate, with no data at all for most taxa, the evidence we have suggests that there have been huge declines, yet most of us have not noticed. It is well understood that we all suffer from shifting-baseline syndrome, whereby we accept the world we grow up in as normal, and also that humans are poor at perceiving gradual change that takes place within their lifetime. The only aspect of insect declines that has impinged on the consciousness of significant numbers of people has become known as the ‘windshield phenomenon’. Anecdotally, almost everybody over the age of about 50 years old can remember a time when any long-distance drive in summer resulted in a windscreen so splattered with dead insects that it was necessary to stop occasionally to scrub them off. Today, drivers in Western Europe and North America are freed from this chore. It seems unlikely that this can be entirely explained by the improved aerodynamics of modern vehicles.

Causes of declines

What might be driving the landscape-scale disappearance of insects? Causes of the decline of wild bees have been discussed more than those of other insects, and most believe that it is the result of a combination of anthropogenic factors, including habitat loss, chronic exposure to complex mixtures of pesticides, and the spread of non-native insect diseases with commercial bee nests [13]. In particular, natural habitats have been cleared to make way for farming, roads, housing estates, factories, golf courses, and a multitude of other human endeavours. Insect populations persisting on small, highly fragmented and isolated islands of habitat, such as the German nature reserves sampled by Hallmann *et al*. [5], are liable to go extinct over time due to the well-understood principles of island biogeography [14]. Species may go extinct on habitat islands decades after the islands were created because the remnant populations are too small and isolated to be viable in the long term, the gradual payback of an extinction debt. This process will be accelerated if islands become polluted with agrochemicals or other pollutants from the surrounding land uses, or are in other ways degraded.

Farming itself has radically changed in the last 80 years. Historically, less intensive farming practices resulted in a patchwork of habitats that were favourable to bees and other insects, including flower-rich hay meadows and chalk downland, fallow fields rich in weeds, and flowering hedgerows separating the small fields. Modern farming in the developed world is typified by large fields maintained as near-perfect monocultures by high inputs of pesticides and fertilizers [15], creating a landscape that is largely inhospitable to wildlife.

Inevitably, the pesticides associated with intensive farming are themselves implicated in driving declines of bees and other insects. Pesticide use is better documented in the UK than anywhere else, and according to government statistics UK farmers applied an average of 17.4 different pesticides to each hectare of land in 2015, using a total of 16.9 thousand tons of active ingredient (i.e. toxins) [15]. Analysis of the pollen and nectar stores of wild or domesticated bees living in or near either farmland or suburban areas (in the UK and elsewhere) almost inevitably finds that their food is contaminated with complex cocktails of insecticides, fungicides and herbicides, usually including neonicotinoids [16–17].

Neonicotinoids are highly potent neurotoxic insecticides, and the finding that they are present in 75% of honey samples collected from around the world [16] demonstrates that bees (and by implication many other insects) are routinely exposed to them. Indeed, there is evidence linking not just bee declines but also those of butterflies and aquatic insects to exposure to this particular class of insecticide (reviewed in [18,19]). It has recently become apparent that exposure to even tiny doses of pesticides can have complex and unpredictable sublethal impacts on insect behaviour, and also that there can be synergistic interactions between different pesticides and between pesticides and other stressors such as disease [18]. None of this is adequately captured by the regulatory process for pesticides which focuses on short-term exposure of organisms to single compounds, and hence it is not currently possible to predict the environmental repercussions of landscape-scale use of large quantities of multiple pesticides [20].

Fertilizer use is also likely to impact on insects. Farmland soils have elevated fertility due to regular applications of synthetic fertilizers, which leads to the dominance of field margin and hedgerow vegetation by a small number of tall-growing, nutrient-loving weed species, reducing botanical diversity with inevitable knock-on effects for insect herbivores and pollinators. For example, Hanley and Wilkins [21] found that hedgerow margins facing farmed fields had much lower floral diversity and attracted far fewer bees than the sides of hedges facing roads. Freshwater habitats draining from agricultural land are similarly polluted, and this eutrophication is highly detrimental to aquatic life which naturally includes a diverse insect community [22].

Although farming tends to be the largest land use and clearly has impacted heavily on insect abundance, there are likely to be many other contributory factors. Our activities produce numerous other pollutants, from heavy metals such as mercury released by mining and industrial processes to the approximately 30 million tons

Figure 2. Bees are master pollinators.
Wild insects such as this buff-tailed bumblebee, *Bombus terrestris*, are vital for pollination of most wildflowers and approximately 75% of the crop types grown by humans (credit: Pieter Haringsma).

of 144,000 different man-made chemicals which we deliberately manufacture and many of which have pervaded the global environment [23]. High levels of polychlorinated biphenyls (PCBs) and polybrominated diphenyl ethers (PBDEs) (along with plastic bags) were recently found in Crustaceans living at the bottom of the Marianas Trench [24]. For the vast majority of pollutants there have been no studies of their impacts on insects, other wildlife, or humans.

Of course the most pervasive man-made pollutants are greenhouse gas emissions leading to climate change. Until recently, direct evidence that climate change has already had major impacts on insect populations was not strong. Hallmann *et al*. [5] incorporated weather variables into their models of changing insect biomass and, while weather inevitably had large effects on catch from day to day, they found that the climate in Germany did not change significantly over this relatively short period (26 years) and so could not explain the decline. There is evidence that the ranges of some insects have begun to shift in response to climate, with European and North American bumblebees tending to disappear from the southern edges of their range, and occupy higher elevations in mountainous regions [25]. There is also evidence that the phenology of some herbivorous and pollinating insects is becoming decoupled from

Figure 3. Insects as biocontrol agents.
Many insects act as important biocontrol agents. The larvae of this hoverfly are voracious predators of aphids (credit: Pieter Haringsma).

that of their host plants; for example some montane plants in Colorado are now coming into flower before bumblebees have emerged from hibernation, when previously they did not [25]. These changes are all fairly subtle so far, although likely to become much stronger as climate change accelerates through the 21st century. However, Lister and Garcia [12] argue that climate has already had profound impacts on Puerto Rican rainforest insects. These forests have not been logged or otherwise directly altered by humans in the last 30 years, and no pesticides are used on or near them. Unlike Germany, the climate of these forests has changed since the late 1970s, with an increase in the mean maximum daily temperature of 2°C, and Lister and Garcia's analyses suggest that this is the most likely cause of the dramatic declines in insect biomass that they recorded.

There are yet more likely or possible contributors to insect decline, many of them very poorly understood. Invasive species have profoundly reduced biodiversity in some ecosystems. Light pollution may have significant impacts on nocturnal insects such as moths [26]. The cognitive abilities of honey bees has been found to be impaired by low electromagnetic fields such as those created around high voltage cables, and it has been suggested that this might have contributed to bee colony losses and more broadly could impact on insect navigation and dispersal [27]. It seems likely that there are other human activities which impinge upon insect health in ways that we have yet to recognize, for the pace of development of technologies far outstrips that of scientists to assess their impacts on the environment, and also far outstrips the ability of nature to adapt.

Consequences

Understandably, few people bemoan the lack of squashed insects on their car, and for many people the idea of fewer insects seems attractive, for insects are often associated with annoyance, bites, stings and the spread of disease. When recently asked about the seriousness of global wildlife declines on national UK radio, medical doctor, professor and well-known TV presenter Lord Robert Winston replied "*There are quite a lot of insects we don't really need on the planet*". This response likely typifies the attitude of many.

Ecologists and entomologists should be deeply concerned that we have done such a poor job of explaining the vital importance of insects to the general public. Insects make up the bulk of known species, and are intimately involved in all terrestrial and freshwater food webs (Figure 1). Without insects, a multitude of birds, bats, reptiles, amphibians, small mammals and fish would disappear. 87% of all plant species require animal pollination, most of it delivered by insects [28] (Figure 2). Approximately 75% of the crop types grown by humans require pollination by insects, a service estimated to be worth $235 to 577 billion per year worldwide [29]. Financial aspects aside, we could not feed the growing global human population without pollinators; billions of people would starve. The importance of insects is often justified in terms of their ecosystem services, which can be ascribed a monetary value. In addition to pollination, insects are important biocontrol agents (often controlling other insect pests; Figure 3), they are intimately involved in the break-down of organic matter such as leaves, timber, animal faeces and carcasses to recycle the nutrients therein (Figure 4), they help to aerate the soil, disperse seeds, and provide products such as silk and honey (reviewed in [29]). These ecosystem services are estimated to be worth at least $57 billion per year in the United States alone [30].

For many insects, we simply do not know what they do. As discussed previously, we have not even given a name to the large majority of species, let alone studied what ecological roles they might perform. As Aldo Leopold

Figure 4. Insect recyclers.
Insects such as this dung beetle perform vital roles in nutrient cycling, helping to break down faeces and dead animals and plants, returning the nutrients to the food chain (credit: Duwwel [Public domain], Wikimedia Commons).

said "*The first rule of intelligent tinkering is to keep all the parts*". We are nowhere near understanding the multitude of interactions that occur between the thousands of organisms that comprise most ecological communities, and so we cannot say which insects we 'need' and which ones we do not. Ehrlich and Ehrlich [31] famously likened loss of species from an ecological community to randomly popping out rivets from the wing of an aeroplane. It might continue to fly for a while, but if enough rivets are removed then at some point there will be a catastrophic failure.

Thus far, I have focused on practical, economic arguments for conserving insect species that either are, or might one day prove to be, valuable to us humans. I would argue that this self-centred approach to conservation is missing the most compelling arguments to conserve biodiversity. Despite what Aldo Leopold said, there are insects which could go extinct without us feeling any economic impact. The St Helen's giant earwig has already done so, and none of us noticed. New Zealand's giant wetas could follow it to oblivion and it is highly unlikely that there would be adverse repercussions. Perhaps we humans could survive in a world with minimal biodiversity; parts of Kansas or Cambridgeshire are pretty close already. Soon we may well have the power to eradicate entire species at will; for example, gene drive technology can exterminate lab populations of the mosquito *Anopheles gambiae*, offering the possibility that one day we might be able to use it to wipe them out in the wild [32]. If we gain that power, should we use it, and where will we stop? Robotics engineers in several labs around the world are developing robotic bees to pollinate crops, the premise being that real bees are in decline and that therefore we may soon need a replacement. Is this the future we would wish for our children, one in which they will never see a monarch butterfly flying overhead, where there are no wildflowers, and where the sound of birdsong and the buzz of insects is replaced by the monotonous drone of robot pollinators? They may be free from malaria, but they will have paid a high price.

Once again I am valuing nature for what it does for us humans. There is one final argument, an unselfish one at last. Do not the rest of the organisms on our planet have as much right to be here as we do?

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