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Modern Insect Extinctions, the Neglected Majority

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Abstract: Most extinctions estimated to have occurred in the historical past, or predicted to occur in the future, are of insects. Despite this, the study of insect extinctions has been neglected. Only 70 modern insect extinctions have been documented, although thousands are estimated to have occurred. By focusing on some of the 70 documented extinctions as case studies, I considered ways in which insect extinctions may differ from those of other taxa. These case studies suggested that two types of extinction might be common for insects but rare for other taxa: extinction of narrow habitat specialists and coextinctions of affiliates with the extinctions of their hosts. Importantly, both of these forms of extinction are often ignored by conservation programs focused on vertebrates and plants. Anecdotal evidence and recent simulations suggest that many insect extinctions may have already occurred because of loss of narrow habitat specialists from restricted habitats and the loss of hosts. If we are serious about insect conservation, we need to spend more time and money documenting such extinctions. To neglect such extinctions is to ignore the majority of species that are or were in need of conservation.

Key Words: coextinction, extinction rates, parasites

Introduction

Knowing how many species we are extinguishing is a basic aspect of our planetary inventory. Pimm and Raven (2000) estimated that 100,000 of every million species could be extinct by 2050 because of habitat loss. What is often glossed over in such estimates is that most of these extinctions are likely to be of insects (Kellert 1993). If 57% of metazoan species are insects (e.g., Stork 1997), Pimm and Raven's estimate equates to 57,000 insect extinctions per million species on Earth in the next 50 years. Other estimates, such as those by Thomas et al. (2004), would yield higher estimates of insect extinctions. The biodiversity crisis is undeniably an insect biodiversity crisis. Yet
insect conservation remains the awkward “kid sister” to vertebrate conservation. Nowhere is this clearer than in what we know, or rather do not know, about insect extinction, particularly for those extinctions that may have already occurred.

If we assume insects have gone extinct at similar rates to other taxa over the last 500 years, we can estimate the number of insect extinctions over that time period based on the extinction rate for well-known taxa. Over the last 600 years 129 bird extinctions, 1.3% of all bird species, were documented (IUCN 2002). Given, say, 3.4 million insect species, we expect roughly 44,000 insect extinctions to have occurred in the last 600 years (see similar estimates in Kellert 1993); 70 insect extinctions were documented over that time period. Considering lists of endangered species reveals a similar discrepancy. Only 37 insect species are currently listed as endangered or threatened in the United States by the Environmental Protection Agency (Redak 2000). If the same proportion of insects were as endangered as vertebrates, we would predict 29,000 endangered or threatened insects in North America (Redak 2000), a possibility that the U.S. Endangered Species Act is incapable of dealing with.

If the above estimates of the number of insect extinctions and the underlying assumption that insect extinction rates are similar to those of other taxa are accurate to even two orders of magnitude, we have missed almost all insect extinctions (and are missing most endangered insects). If such estimates are wrong, we are grossly misjudging how many species are currently at risk of extinction. Understanding the discrepancy between estimated and observed insect extinction rates thus seems worth considering. What accounts for the tens of thousands of expected but undocumented insect extinctions? What does this discrepancy mean? How important is it to our understanding of extinction and the future of ecosystems?

These should be questions at the heart of species conservation, yet they have hardly been addressed. No peer-reviewed articles have been published reviewing modern insect extinctions, and no estimates of global extinction rates have explicitly focused on insects. Here I take a case-study approach to address whether and why insect extinctions might differ from those of better-studied taxa and how we might better estimate the magnitude of insect extinctions. The extinct insects do not form a data set per se because we have documented so few. Nonetheless, we may be able to learn a fair amount from them.

The “Data Set” of Extinct Insects

Little has been recorded about the demise of extinct insect species, even for observed extinctions. The only information in the IUCN database for extinct insects consists of the country and region in which it lived and some-times the year in which it was described. Outside of the IUCN database, additional information on these species is scarce, typically consisting of only the original description of the species and a few lines in a subsequent revision of the group. Occasionally authors considered the causes of an extinct insect species’ demise (e.g., Rentz 1977; Liebherr & Polhemus 1997; McCafferty 2001), although even in these cases no additional information was incorporated into the IUCN database.

Undoubtedly one reason so few insect extinctions have been documented is understudy. Fewer than half of all metazoan species are described, and even for described insect species most are known from a single specimen and site (Stork 1997). Even for large insect species on small islands, documenting extinction with any certainty is difficult because so little is known about the habitat preference and seasonality of most insect species (e.g., Priddel et al. 2003). Many scientists know of insect species they assume are extinct, but they have not been able to search for them with the conclusiveness the IUCN list requires. Sometimes these “missing” species make it into publications (e.g., McCafferty 2001) before they are listed as extinct, but more often than not these missing species are known only by the experts on the group. The difficulty in documenting insect extinctions is apparent even within the insect extinctions that have been documented (Stork 1997; McKinney 1999). Most documented insect extinctions are from well-studied taxa in well-studied regions (Mawdsley & Stork 1995), simply because these are the species whose absences we are capable of noticing. Fifty-five of the documented extinctions are from the United States. Thirty-eight of these extinctions are from Hawaii, an island group that is exceptional only in that it was studied early enough to document insects before they were gone (Priddel et al. 2003). Insect extinction rates could be higher on islands than on mainlands, as is the case for birds (e.g., Manne et al. 1999), but habitats on islands may also just be easier to search completely (Mawdsley & Stork 1995). Most of the documented extinct insect species not from Hawaii are from continental North America (IUCN 2002). Taxonomically, most observed insect extinctions are from charismatic clades (Mawdsley & Stork 1995). More than half of all recently documented insect extinctions are of Lepidoptera (37 species; IUCN 2002), arguably the best-studied insect taxon.

Although the difficulty of studying insect extinction may account for much of the discrepancy between expected and observed extinction rates for insects, it may not be the whole story. Some evidence suggests that insects may actually be less extinction prone than other taxa or at risk from different factors than other taxa. Even insect taxa that have been relatively well studied show lower rates of historical extinction in the United States than birds over the same time period. We have not yet succeeded in extinguishing even 1 of the roughly 111 species of tiger beetles collected in the continental United States.
(although several are close; Pearson & Cassola 1992), and we have not extinguished any species of odonates from the same region (Liebherr & Polhemis 1997). Only one species of Macrolepidoptera in the United States appears to have gone extinct (IUCN 2002). Mawdsley and Stork (1995) calculated future extinction rates of a variety of taxa based on lists of endangered species. They predicted that for the United Kingdom regional extinction rates for insects are one-fourth to one-tenth those of birds (Mawdsley & Stork 1995). Although even a 10-fold difference in the extinction rates of birds and insects does not nearly account for the differences between estimates and observed numbers of insect extinctions, it suggests insect extinctions may differ in important ways from those of birds and mammals.

Insect extinctions might differ in rate and other attributes from those of other taxa for a variety of reasons. Because of their small size, insects might require smaller total habitat areas for a given population size (e.g., Blackburn & Gaston 1997). Alternatively, the factors driving insect extinctions may differ in both kind and relative importance from those driving the extinctions of other taxa. Many documented insect extinctions appear to be due to the same factors that drive vertebrate extinctions and hence represent extinctions that could be prevented by conservation measures targeted at vertebrates. For example, eight Singaporean species of phasmatids appear to have gone extinct because of the same habitat loss and overharvest (for medicines) affecting vertebrates in the region (Seow-Choen 1997). Aquatic insects, like aquatic vertebrates, are particularly at risk, with four mayflies likely extinct from the United States alone (McGafferty 2001). Other documented insect extinctions, however, are due to factors likely to play only a minor role in the extinctions of vertebrates or plants or occur in places or at spatial scales different from those of vertebrates and plants. The list of documented insect extinctions contains apparent examples of both extinctions of extremely narrow habitat specialists and coextinctions (extinction of affiliates with the extinction of their hosts). Importantly, both these groups of extinct species are likely to be missed by conservation plans and studies directed at vertebrates and plants. Thus, I focused on these forms of extinction in insects, their potential significance, and how we might better quantify their magnitude.

**Narrow Habitat Specialists**

The Antioch sand dunes are an emblematic case study in the extinction of narrow habitat specialists from restricted habitats, typically not considered for conservation. The Antioch Dunes in California (U.S.A.) were originally contiguous with the Mohave Desert to the south. Prehistorically, climatic changes isolated the dunes from the Mohave Desert and thus isolated the species that lived on the dunes. As a result, the species in the sand dunes are not coastal dune species but desert species, many of which are endemic to the sand dunes. Historically, the dunes stretched roughly 9 km along the San Joaquin River. Fewer than 22 ha of this original habitat remain (USFWS 2001).

In the 1960s, Dave Rentz found one individual of a new species, *Neduba sp.*, in a specimen drawer. The specimen had been collected years earlier on the Antioch Dunes but never described. The new species was unique in the morphology of its genitalia and its size. Rentz went to the Antioch Dunes but could find no living individuals. After several years of searching, he described the species as *Neduba extincta*, the extinct neduba katydid and it was put on the IUCN list of extinct species (Rentz 1977). Not long thereafter, entomologists began to look for other historically recorded insect taxa on the sand dunes (Powell 1978; USFWS 2001). We now know there were at least eight insect species endemic to the dunes. Three of those species, *N.extincta*, Antioch robber fly (*Cophura buri*), and Antioch sphecid wasp (*Phialantbus nasalis*), appear to be extinct (e.g., Powell 1978). The remaining species are listed as endangered or are proposed for listing, but by any measure they are threatened (USFWS 2001).

The story of the Antioch Dunes is not an isolated one. It instead seems to represent what has probably occurred or is occurring in many isolated habitats that, like Antioch, are too small to have endemic vertebrates but not too small for endemic insects (e.g., Powell 1978). Vertebrate conservation plans or plans based on vegetation type would probably not have conserved any of the Antioch Dune endemic insects because no vertebrate or plant species are endemic to the dunes.

Fortunately, the Antioch site is protected now, because of the presence of an endemic butterfly subspecies and an endemic plant subspecies (Powell 1978; Mattoni et al. 2000; USFWS 2001). In many cases habitats with endemic insects but few or no endemic vertebrates or plants are ignored and unprotected. Recent studies of sand plain habitats in Connecticut (U.S.A.) included on the National Vegetation Classification System as “sparsely vegetated sand dunes” revealed a diversity of insect species apparently restricted to particular sand dune types not distinguishable based on vegetation (D. Wagner, unpublished data). Few plant species are endemic to these habitats and in many cases the plant species are primarily invasive, yet from an entomological perspective these habitats should be some of the most important conservation targets in New England. They remain unprotected even though the cost of conserving such reduced habitat types is often relatively small (e.g., USFWS 2001), particularly when compared to the millions of dollars that can be spent each year on captive breeding programs for individual vertebrate species (e.g., the Californian Condor [*Gymnogyps californianus*]; Snyder et al. 1996).

The Antioch sand dunes and the New England sand dune systems are two cases where insects appear to...
have both narrower and spatially different habitat requirements than do vertebrates and plants. Insects may generally be more likely to have narrower habitat specificities or different spatial patterns of habitat specificities than other taxa (and hence be at greater risk of extinction or in need of different conservation measures). Insect species might be expected to have smaller geographic ranges than other taxa if they are able to pack more individuals into a smaller area, have a smaller geographic range for a given population size, and hence be endemic to more geographically restricted, or patchy, habitat types.

Anecdotal evidence and the field knowledge of many entomologists support the hypothesis that insects tend to have smaller geographic ranges with different range midpoints than do other taxa, but more general data are scarce. Some evidence exists that the average range sizes of insect taxa are smaller than the average range sizes of vertebrates (Lees et al. 1999). Comparison of the minimum range sizes of insects and other taxa would depend on much finer scale data than are typically available. Studies such as Yeates et al. (2002) begin to address this deficiency. Yeates et al. (2002) found that both the absolute number of species and the percentage of species endemic to particular upland wet forests in northeast Australia were much higher for flightless insects than they were for vertebrates, an indication of the relative range sizes of the two groups (Yeates et al. 2002). Nine of the 14 uplands considered contained endemic wingless insects but no endemic vertebrates.

Work like that of Yeates et al. (2002) raises the question of whether the smallest viable geographic ranges of insects are generally smaller than those of vertebrates and, if so, how great the consequences of this trend for conservation will be. To the extent that minimum viable range sizes of species are a function of minimum viable population sizes, answers to these questions will depend on how tightly coupled body size and population density are at large scales and whether the relationship between the two variables is linear (e.g., Blackburn & Gaston 1997; Ackerman & Bellwood 2003). If we are serious about conserving insects, we need to obtain answers to these questions, even if for only a few well-studied taxa and regions.

Although many extinct, narrow-habitat specialists had historically small geographic ranges and low local abundances, this was not the case for all species. Several documented extinctions were of insect species with narrow habitat preferences in at least one life stage but with high local densities and often large geographic ranges. The Rocky Mountain locust (Melanoplus spretus) appears to be one such case. The Rocky Mountain locust was the single largest barrier to westward expansion in the United States in the 1800s. National programs were developed to “exterminate the locust” (Lockwood 1989). Lockwood and DeBrey (1990) plausibly argued that these efforts, combined with destruction of the floodplain habitats (by both extirpation of beavers and introduction of cattle) appear to have led to the locust’s extinction. Although the locust’s range stretched across the United States, its breeding grounds were a restricted habitat type and occupied a much smaller, patchier area. The last individual locust collected in 1902 is among just a handful of individuals preserved in museums. When the locust was abundant few apparently thought it was worthwhile to preserve specimens (Lockwood & DeBrey 1990).

Although the Rocky Mountain locust’s combination of relatively narrow habitat specificity, large geographic range, and high abundance is not unique to insects, the force with which we attempted to extinguish the locust may now be. Although historical extinctions of vertebrates were often intentional (e.g., Bulte et al. 2003), modern extinctions of vertebrates rarely are. Humans appear to have intentionally extinguished a variety of insect species, including several species of Hawaiian moth (e.g., Howarth 1991). Most of these species appear to have been locally abundant but restricted in their habitat preference. Whereas such intentional extinctions are largely in the past for vertebrates, they may not be for insects. We are still willing to extirpate and even extinguish insects when they cause economic hardships. Pest species are exempt from the U.S. Endangered Species Act, so even if, for example, the Rocky Mountain locust were rediscovered it would probably be extinguished. The combined forces of unintentional and intentional human disturbance may put even abundant insect species with narrow habitat specificity at more risk than vertebrate species with similar ranges and habitat requirements.

Cases in which we are intentionally attempting to extinguish abundant insects may be relatively rare, but cases where we, as biologists, turn a blind eye to the consequences of our actions for abundant insect species abound. Such inaction is all but willful. Captive-bred animals (Windsor 1995; Gompper & Williams 1998; Perez & Palma 2001) and endangered plants (Lesica & Athowwe 2000) are often deloused or dosed with pesticides without regard for the fate of their parasites. Such species are not intentionally being extinguished, but they are ignored in a way that increases their probability of extinction. Intentional introductions of biocontrol agents appear to have led to the local, if not global, extinction of a variety of insects. Eighty percent of the larvae of three native Saturniid moths in New England (U.S.A.) are infected with parasitic flies introduced as biocontrol agents, with negative effects on the populations of the Saturniids and their native parasites, many of which are missing (Boettner et al. 2000). Similar stories are also being revealed in Hawaii (e.g., Henneman & Memmott 2001). Amazingly, in many places, including the United States, the effects of insects introduced for biocontrol on other insects do not need to be tested (e.g., Boettner et al. 2001).

Extinctions of relatively abundant species with narrow habitat specificities make up a relatively large percentage
of documented insect extinctions (roughly 1 in 10, depending on how one defines abundant). Extinctions of such abundant species are probably overrepresented in lists of extinct insect species simply because we were more likely to have noticed that they went extinct. This says something about how we value insects. Extinctions of abundant insect species are perhaps not surprising because of the low value people in Western societies give insects (e.g., Kellert 1993). If the only reason we conserve species is for aesthetic and cultural values, perhaps ignoring insects is a logical way to allocate conservation dollars. However, if we really conserve species for the reasons we tend to list when we give talks and write textbooks (ecological functions, potential uses, and inherent values of species; reviewed for insects in Kellert 1993), we would be hard pressed to value a locust less than a condor or a tiger.

Coextinction

Because most insect species are parasites, the most restricted habitat occupied by many insects is arguably their host. Stork and Lyal (1993) highlighted the possibility that many parasites may go extinct when their hosts go extinct, a process they termed coextinction. They used the example of two louse species thought to have gone extinct with the Passenger Pigeon (Ectopistes migratorius). For a time, both Passenger Pigeon lice were on the IUCN list as extinct, but both species have since turned up on living pigeons (Price et al. 2000; Dunn 2002), leaving us with no well-documented cases of the coextinction of a vertebrate parasite. Subsequent studies have been reluctant to declare species extinct in light of the possibility that they might persist on alternate hosts. At least nine bird lice are thought to have been host specific on bird species that are now extinct (Koh et al. 2004a). Similarly, a species of ferret louse, Neotrichodectes sp., and a species of protozoan may have gone extinct with the black-footed ferret (Mustela nigripes) either when ferret populations were reduced or when the ferrets were deloused during captive breeding (Gompper & Williams 1998). Neither the nine bird lice nor the black-footed ferret louse is listed as extinct or even threatened (IUCN 2002). These lice are some of the many species of animal parasites biologists suspect may have gone extinct but have been reluctant to dismiss. The most endangered feline in the world, the Iberian lynx (Lynx pardinus), appears to be the sole host of the most endangered feline louse (Perez & Palma 2001), but this is just one of what are probably thousands of such cases.

The only well-documented case of extinction of an insect with a change in the abundance of its animal host (albeit a local rather than global extinction) is that of the large blue butterfly (Maculinea arion). As larvae, large blue butterflies are fed by workers and prey on larvae of a single species of host ant, Myrmica sabuleti. Biocontrol of introduced rabbits (Oryctolagus cuniculus) in the United Kingdom with Myxoma virus appears to have reduced the occurrence of open habitats, which the rabbit grazed. The host ant decreased in abundance as the amount of open habitat decreased, which in turn appears to have led to the extinction of the large blue (e.g., Elmes & Thomas 1992). Whether the extinction of the large blue led in turn to the extinction of any parasites the butterfly might have had remains undocumented. The example of the large blue serves to demonstrate potential extinction cascades and that parasites can go extinct even if their hosts simply decline in abundance.

Defined broadly, parasites also include herbivores, and a few cases of parasite extinction have been documented for host-specific plant feeders such as some butterflies and moths. When the chestnut blight attacked chestnuts (Castanea dentata Marsh.) and reduced them to thousands of fruitless wisps, Opler (1978) speculated that seven species of Lepidoptera might have been lost. Four of those species were subsequently found (P. Opler and D. Wagner, personal communication), but three species remain missing and are presumed extinct (IUCN 2002). Host-specific beetles, parasitoids, and other groups may have also been lost with the chestnut decline, but this remains to be investigated. More recently, Koh et al. (2004a) suggested that coextinction cause by the loss of host plants accounts for many of the regional extinctions of butterflies from Singapore.

Although few examples of coextinction have been documented, the mathematics of the process is straightforward. If one knows the average number of parasite species restricted to a single host species in a given taxon, then one can predict the number of host-specific parasites expected to have gone extinct per host (Koh et al. 2004b). Parasites dependent on two or more species in their most host-specific life stage are statistically more vouchsafed against extinction than more host-specific species but are nonetheless still at risk (Koh et al. 2004b). Recently, Koh et al. (2004b) used host specificity distributions for selected affliliate taxa (a general term including both parasites and mutualists) to estimate the number of historical extinctions due to coextinction, and the number of species likely to go extinct through coextinction were all endangered vertebrates and plants. They found that no fewer than 5000 insect species are likely to be endangered because of the endangerment of their hosts, and that no fewer than 100 species of beetles, lice, and butterflies alone are likely to have gone extinct because of the extinction of their hosts during the last 200 years.

The Koh et al. (2004b) estimates of coextinction rates take into account only extinctions likely to occur when hosts go extinct globally. Parasite and mutualist extinctions can also occur even if host species do not become extinct globally but are simply reduced in abundance and brought into captive breeding or seed bank programs and
stripped of their parasites. Given the large number of taxa recommended for captive breeding programs (e.g., 34% of the 3550 species considered by Seal et al. 1993), the losses from captive breeding alone could be hundreds of species. The potential magnitude of coextinctions should make them a key focus of conservation biology, yet the process of coextinction has been little studied (Koh et al. 2004b). Windsor (1995) listed the many reasons parasites deserve more attention from conservation biologists in an article entitled “Equal Rights for Parasites.” These pleas seem to have been ignored. For example, I was able to find only two articles on lice in Conservation Biology, Biological Conservation, or Biodiversity and Conservation in the last 10 years, despite the fact that endangered bird and mammal parasites, such as lice, almost certainly outnumber endangered birds and mammals. Even if we persist in ignoring the conservation of parasites, it still behooves us to document parasite extinctions where and when we can. We need to understand parasite extinctions if only because of their likely high frequency.

Conclusions

A consideration of what we know about insect extinction seems to hold a number of lessons worth bearing in mind. First, although we know a fair amount about the modern extinctions of vertebrates, we know little about those of insects. This is not surprising, but it is worth reiterating because insects will almost inevitably represent most extinctions in the coming years. Second, although we estimate that most extinctions have been of insects, our greatest loss of evolutionary history is likely to be through the loss of insects, or invertebrates more generally. Our greatest loss in terms of number of species is likely to be through the loss of narrow habitat specialists and coextinction, but insect extinctions may also differ in other important ways. For example, social insects appear to be disproportionately susceptible to extinction because of their small effective population sizes (Chapman & Bourke 2001), but sociality in vertebrates seems unlikely to account for much of the variation in extinction risk.

Documented insect extinctions hardly form a good data set from which to extrapolate and they may not be a random subset of all extinctions (they are most certainly not in their taxonomic focus), but if these trends are representative they are troubling. We need to focus more funding and research on conserving insects, but we also need to record the extinction of insects. Our greatest loss in terms of number of species is likely to be through the loss of insects. Our greatest loss of evolutionary history is likely to be through the loss of insects, or invertebrates more generally. Without rekindling the old debate about whether small or large species run the world, it is safe to say that most ecological processes are at least partially mediated by insects. Thus, losses of ecosystem function due to the losses of insect species will arguably be potentially great.

The key to understanding insect extinction is better documentation of the process itself. Documenting insect extinction serves the dual role of educating scientists about extinctions and providing concrete examples to the public of what we are doing. How might we better document insect extinctions? One pictures a thousand biologists running through the forests and savannas searching for their favorite species. Such time in the field will undoubtedly turn up some missing species, but more directed searches might prove more fruitful. In particular, regions with historical inventories should continue to be repeatedly inventoried, a task that would prove easier given persistent funding for parataxonomists (Goldstein 2004). Scouring skins of extinct vertebrates may permit discovery of many extinct invertebrates. Because we have no clear examples of coextinction of invertebrates from animal hosts, such examples would be of uncommon importance. If known extinct insects are at all representative, restricted habitats such as sand plains are also important places to search for species collected historically but perhaps not known from recent collections.

Conservation measures taken for vertebrates and those needed for insects (or invertebrates more generally) are not always the same. Species with endangered hosts may often be conserved by conserving the host, but not if pesticides continue to be used on rare plants and vertebrates (Lesica & Atthowe 2000). However, species with habitat types too small to have endemic plants or vertebrates are unlikely to find much in the way of conservation monies. If we are serious about conserving species diversity and not just charismatic species diversity, conserving a few key and tiny habitat types such as the Antioch Dunes is likely to save more species than will the millions of dollars spent on vertebrate umbrella species. If we are losing many hundreds of species from tiny, ignored habitats, our relative disinterest in the conservation of these habitats is a measure of how little we really value insects and their conservation. We can decide to value insects much less than vertebrates and plants, but we should make this decision consciously and not through neglect.

Acknowledgments

Literature Cited


