Identifying predictors of insect abundance

Insects are among the most abundant groups of terrestrial animal.[1] Due to this, any view concerned with the moral consideration of sentient beings, especially in the wild, needs to pay a lot of attention to the situation of these animals. Insect sentience is the subject of ongoing scientific investigation, and there is some important evidence for them being sentient, because they have highly developed sensory abilities and nervous systems. In general, insects live complex and active lives for which sentience may be adaptive. Some insects also show complex behavior, such as the dance language of honeybees. This suggests their brains may also be able to support sentience. If, as this evidence indicates, they are sentient, then given the relevance of sentience, their sheer numbers make them very important in our decisions concerning how to best improve the situation of animals. It is been estimated that there may be approximately 10^{18}insects.[2]

Understanding the present drivers and correlates of insect abundance might be helpful in comparing different situations with regard to the total amount of insect suffering present or possible in them. Accordingly, it can also be useful in predicting or measuring the consequences of actions we could take that could be beneficial or harmful to them.

The study of insect populations can also be relevant to the study of the wellbeing of other animals in different ecosystems, because insect populations can significantly affect the other animal populations that live in the same ecosystem. But the main way insects can contribute negatively or positively to the overall levels of wellbeing in an ecosystem is quite direct: through their own levels of suffering or positive wellbeing.

In order to properly assess the levels of suffering and pleasure insects can have at a very large scale, it would be useful to have a globally applicable, quantitative model of insect abundance that accounts for the varying importance of the main limiting factors shaping their populations. In the

nearer term, it will be important for ecologists to identify a consistent way of measuring insect abundance, or else develop ways of statistically correcting for known error-rates/biases between methods, in order to improve the comparability of results from different locations and for different species. One example of a study moving in this direction has been carried out considering only flying insects in Germany.[3] While the study is limited in scope, it places an emphasis on standardized data collection and carries out a factor analysis to determine the most powerful predictors of insect abundance within its study system. Similar projects could be carried out on a wider scale. We will see below what kind of indicators such a model could use.

Ecology of Insect Communities

It is estimated that there are several million insect species on earth, most of them undiscovered by humans. This huge diversity goes hand in hand with specialization in a wide variety of ecological niches. Insects may feed on dead (detritivores) or living (herbivores) plant parts, or other animals (predators and parasites). There are also mixed feeders that shift between food sources over the course of their development. Insects are so abundant and many of them are so specialized that most of the bigger plants and animals have insect parasites or herbivores specialized to feed exclusively on them. Insects are also adapted to a wide variety of climates and biomes, ranging from the tropics to tundra ecosystems. This diversity makes it impossible to identify a single indicator that will apply to all insect species. However, it is plausible that trends in overall insect biomass could be identified, without discriminating between species. This would be helpful as it would still allow us to make generalizations, given the vast number of individuals involved. Of course, biomass itself isn’t directly relevant; the number of individual insects is. However, given than the actual number of insects may be difficult to find, biomass may be the best measure available.

Terrestrial ecosystems can be divided into three parts: soil, litter, and canopy. Insects are very numerous in the canopy, while the majority of soil organisms are other arthropods like mites and springtails, as well as various groups of worms.[4] The litter is inhabited by both insects and other arthropods. Many of these insects are herbivores, either chewing leaf material, sucking plant juices, or feeding on seeds, nectar, or pollen. In some ecosystems, insects are even the dominant herbivorous animal group in terms of biomass consumption. It has been estimated that around 80% of the total plant biomass consumed in an American short grass prairie is eaten by grasshoppers.[5]

Identifying predictors of insect abundance

Indicator species

In order to efficiently monitor trends in biodiversity and habitat quality, ecologists have developed the concept of indicator species. Indicator species are selected as representative of a larger taxonomic or functional group whose fates are thought to be correlated.[6] must be relatively easy to study/survey, but other criteria vary according to the objectives of a given study. For example, butterflies and birds both correlate to some extent with greater invertebrate abundance; both are highly mobile, allowing them to track appropriate habitat or feed sources. However, butterfly numbers vary over a much smaller spatial and temporal scale than those of birds due to their smaller size and shorter generation times, although finer-scale data come at the cost of more noise, because butterfly populations are more likely to be devastated by a storm or other unrepresentative event.[7]

The use of indicator species, while practical, has significant limitations which must be acknowledged.[8] Most notably, they are likely to be environment-specific. A species can only be used as an indicator within its own geographic range, but even there, the strength of its correlation with others may vary with habitat, climate, and biotic interactions such as predation and parasitism. In general, indicator species are likely to indicate most effectively in environments that are not hostile for them, as in the case of temperate grasslands for butterflies.[9] Future environmental changes might change the correlations. Finally, one's chosen method for surveying abundance might be inherently biased, leading to the identification of an indicator species that will not be as effective under a different survey method.[10] There are no objective selection criteria for indicator species, placing the onus on researchers to be as transparent as possible about their reasoning, including how they might have compromised precision for practicality. Most of these limitations apply to potential abiotic indicators as well, as will be discussed below.

Abundance-limiting factors

The performance of an indicator depends on the precise limiting factor(s) regulating the population in a given environment. There are three basic ways populations can be limited: bottom-up control, top-down control, and environmental factors. Bottom-up controlled populations are limited by resources. This includes abiotic consumables like water, inorganic nutrients, and sunlight as well as the availability of plants, animals, and other organisms as food sources. Top-down controlled populations, on the other hand, do not grow over certain numbers due to predation or parasitism. Environmental factors of population control include static variables like relative humidity, temperature, UV radiation, suitable habitat, and toxic chemicals, which constrain, but are not competed over, as resources. A promising strategy to find reliable predictors of insect abundance is identifying the most important limiting factors of insect populations. These basic rules of

population control do, however, also apply to the limiting food sources and predators of insects, so the complexity of the question grows rapidly as more species and/or ecological variables are taken into account.

The concept of trophic cascades was introduced to express how a shift in the primary factor constraining the size of one population can lead to similar changes in the populations of different species with which they interact.[11] Meta-analyses of time-series data suggest that top-down regulation by predators and parasites is more important than bottom-up factors among herbivorous insects as a whole, and far more important than in most other animal groups.[12]However, the predominance of top-down regulation is not universal, and species may depart radically from that trend, such as the moth *Tortix viridana*.[13]

Top-down control

High insect abundance and diversity supports a wide variety of insectivorous predators, parasites, and pathogens. Just like insects, birds are ubiquitous across almost all biomes and they rely heavily on insects for food. 90% of all bird species (dropping to 60% in the tropics) are insectivores whose diet consists of 75% or more insects or other arthropods.[14] If we assume bottom-up control of bird populations, there should be a strong correlation between insect and bird abundance. This correlation would increase when considering only insectivorous birds.

Birds are well-researched, and measuring their abundance is comparatively easy and regularly done. There are also a number of experiments that show a substantial increase in arthropod abundance with the exclosure of birds.[15] Birds also prey on spiders who themselves prey on insects. In some environments, depending on how large a fraction of the birds' diet is made up of insects and the relative efficiency of insectivorous spiders, this could counteract the effects of birds on insect abundance.[16] It is also possible that bird numbers are controlled by factors other than food abundance. In certain regions, they could just as well be top-down controlled by predators (e.g. cats) or environmental factors (e.g. lack of suitable habitat). Birds might also focus their predatory effort on specific taxa, like flying insects, and thus not correlate so well with total insect abundance.

In tropical forests, bats may kill more arthropods than birds.[17] Bats also inhabit temperate forest ecosystems and may kill a very important number of insects there, too. However, bats are probably less suitable than birds as indicators given their nocturnality, which makes them harder to survey, as well as their more restricted geographic range. Many other animal groups consume

insects, including many amphibians and reptiles, and some mammals. However, birds, spiders, and bats are probably the most wide-ranging insectivores, which should make them better indicators than less mobile animals.

Members of most insect species host several parasite species at once, some of them insects themselves. It has been suggested that a major limiting factor of grasshopper populations in cold and moist years is fungal infections, which kill a large number of these animals.[18] Pathogens and parasites thus play an important role in impeding the growth of insects. However, wildlife diseases are difficult to survey, making them inferior indicators of insect abundance.

Bottom-up control

Since most insects are detritivores or herbivores, the abundance and quality of dead and living plant tissue is of great importance for bottom-up control. This includes the total biomass production as well as the quality of the plant tissue determined by plant defenses and nutrient content. Plant parts contain structural (e.g. lignin) and toxic (e.g. nicotine) chemical compounds, as well as physical defenses to reduce herbivory. Probably most important for the nutritional quality of plant tissue is the amount of extractable chemical energy and the protein content. Reproductive organs like seeds and pollen, followed by leaf tissue, have the highest nutritional value. Wood, roots, and dead plant parts contain almost no protein and their components are difficult to break down and use as an energy source.

Net primary productivity (NPP) refers to the total energy and carbon budget available in an ecosystem for fueling biological processes. Energy and carbon ultimately come from photosynthesis, meaning that NPP reflects the abundance and bioavailability of plant tissue. NPP varies widely over the surface of the earth, peaking in the tropics and bottoming out in cold or hot deserts. That is to say, NPP is highest in warm and wet conditions.[19] Herbivorous insects are primary consumers, some of the first animals to get their mouthparts around the products of photosynthesis before they themselves are eaten and pass on that energy on to another. Detritivorous insects largely eat plant material that other herbivores are unable to digest or not interested in. However, the share of NPP consumed by insects varies greatly between environments. In temperate ecosystems, studies have attributed merely 10% or less of terrestrial temperate-ecosystem primary consumption to insects, except in restricted scenarios like outbreaks of moths or locusts.[20] This is attributed to top-down control of their populations, as discussed above, or limitation by food quality over quantity, as the diets of many insect species are highly specialized.[21] However, NPP is a fundamental determinant of all animal biomass, and thus of the total number of animals that there are, including the insects' predators. Therefore, this top-down control has more to do with the proportionality between NPP and insect abundance. If

the percentage of NPP consumed by insects is constant or predictable across biomes and ecosystems, NPP could serve as an excellent predictor of insect abundance. Again, it is ultimately the number of individuals that is significant, rather than biomass, but it is more difficult to find the number of individuals, so we may have to rely on biomass as an intermediate measure in some cases.

The Normalized Difference Vegetation Index (NDVI) is an index calculated from satellite image spectra. By tracking differential absorption of light wavelengths associated with photosynthesis ("photosynthetically active radiation"), NDVI essentially captures how "green" an area is, providing a good proxy for NPP. Indeed, NDVI has been used successfully as an indicator for many different insect carriers of disease, including malarial mosquitoes and flies.[22] Nearly all work relating NDVI to insect abundance has been done on flies, but this method could work in the case of other insects as well. Low-lying cloud cover might also be developed as a proxy for NPP, because it is closely related to the process of evapotranspiration, by which water returns from soil to the atmosphere, vastly accelerated by plants.[23]

Environmental factors

Insects live in a wide variety of habitats with extreme variation in environmental factors such as temperature, humidity, precipitation, radiation, and wind speed. Such variation in conditions could be associated with similar variation in abundance. On the other hand, considering the diversity of insects, environmental factors might change species compositions while having comparatively small effects on overall insect abundance. For example, it has been found that wind speed is a good predictor of the abundance of a fly, *Culicoides imicola*, in Morocco and the Iberian Peninsula,[24] but wind speed is likely to affect flying insects disproportionately.

Environmental factors might also impact insect abundance indirectly by limiting biotic factors (e.g. extremely low temperatures could lead to a lack of plants to eat). Most environmental factors are also influenced by biological activity, blurring their distinction. For example, humidity, temperature, precipitation, and radiation at ground level are all both causes and consequences of foliage cover, interacting with bottom-up factors that might regulate insect abundance.[25]

Nitrogen availability is thought to be the limiting factor of NPP in most terrestrial ecosystems, with the exception of lowland tropical forests.[26] states that insect populations in nitrogen-limited communities are likely to be controlled bottom-up by (plant) food availability. Increases in insect abundance following the addition of nitrogen to an ecosystem (e.g. via fertilizer) have been well-documented, and seem to be mediated by plant abundance and diversity.[27] However, NPP and nitrogen availability can also become out of sync, as nitrogen limitation reduces the quality of

plant material for herbivores. The long-term FACE field experiments, where plants are grown under elevated CO_2, have shown that trees under these conditions are more productive in terms of biomass, but their leaves contain less protein (higher C/N ratio) and the extra biomass they produce is low in nitrogen.[28] Thus, insect abundance (and heterotrophic life in general) is probably even more strongly limited by nitrogen availability than NPP. Since CO_2 is generally well-mixed in the atmosphere, NPP should remain a good indicator of insect abundance at least between regions with similar levels of nitrogen-availability/limitation, although the rate at which insect abundance scales with NPP may be lessened if the nitrogen component of plant biomass decreases under higher-CO_2 conditions.

Conclusion and suggestions for further research

The ultimate goal for this line of research within welfare biology should be a globally applicable, quantitative model of insect abundance that could show how a variety of limiting factors can affect it in different ecosystems.

Right now, we are still very far away from such a causally explicit model. However, basic predictors like NPP, which can be estimated easily through satellite image spectra, seem to be very effective at predicting insect abundance on a regional scale. NPP-based models might even be useful for other areas of welfare biology; for example, they have been used to predict overwintering sites for migratory birds based on the finding that NPP correlates with survivorship.[29] The effect that rising atmospheric CO_2 concentrations might have on the strength of this correlation therefore also deserves continued study.

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