SPECIAL ISSUE: INSECT EXTINCTIONS

# Using network ecology to understand and mitigate long-term insect declines

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## Introduction

Insects represent one of the most diverse groups of animals on Earth with estimates ranging from 1.5 to 5.5 million species, but many taxa remain poorly studied, which is concerning given their importance for many ecological processes. Indeed, fewer than 1% of the 1.4 million described invertebrate species have been assessed by the IUCN, but of those that have ~40% are considered threatened (Dirzo *et al.*, 2014). Furthermore, insects are embedded in complex networks of ecological interactions (Pocock *et al.*, 2012) of which we know even less. Case studies highlighting substantial insect declines around the world have raised alarm, with a recent meta-analysis showing an average decline of terrestrial insect abundance of ~9% per decade (though an apparent increase in freshwater insect abundances) (van Klink *et al.*, 2020).

Some of the best datasets of insect time series, such as the UK's Rothamsted Insect Survey (RIS) and Butterfly Monitoring Scheme (UKMBS), have been crucial for understanding long-term insect population trends (Conrad *et al.*, 2006; Bell *et al.*, 2020), as well as correlatively identifying the major threats to insect biodiversity (Wagner, 2020). The original purposes of insect biomonitoring schemes are varied and often target particular groups (e.g. agricultural pests) and at certain stages of their life-cycle (e.g. migration). For some schemes, considerable non-target insect 'bycatch' is routinely collected and stored (see Hribar, 2020) but excluded from analyses due to lack of resources and/or expertise, or discarded outright. In our opinion, insect bycatch data provides an exceptional but as yet untapped resource for better understanding insect declines. Indeed, recent advances in Next Generation Sequencing can

overcome many of the previous obstacles in processing bycatch and when combined with new methods in network ecology (Evans *et al.*, 2016), moves towards a more mechanistic understanding of insect declines and the cascading effects on biodiversity and ecosystem functioning.

Ecological networks describe the interactions between species, the underlying structure of communities and the function and stability of ecosystems (Montoya *et al.*, 2006). Most network studies to date have focused on bipartite interactions, in particular mutualisms (e.g. plant-pollinator interactions) and to a lesser extent antagonisms (e.g. host-parasitoid interactions) and commensalisms. They are particularly well suited to the study of species loss and how this can cause extinction cascades across ecosystems (Pocock *et al.*, 2012; Evans *et al.*, 2013; Kehoe *et al.*, 2020). While new network construction methods are gaining traction (e.g. Staniczenko *et al.*, 2017; Evans & Kitson, 2020), there is a dearth of understanding of the complex ways in which insects interact, and long-term species-interaction datasets are scant, which currently limits our ability to use networks predictively.

We contend that insect monitoring schemes, especially those with preserved sample archives, hold considerable potential for the construction of highly-resolved, long-term ecological networks, which can then be uniquely used to examine the impacts of environmental change on network structure, complexity, and robustness (a measure of the tolerance to species extinctions) across scales, the impacts on ecosystem functioning (especially pollination, pest regulation) and new restoration methods. Here, we highlight the added value that network ecology brings to insect biomonitoring schemes, particularly in the context of understanding insect declines. We briefly discuss: (i) insect data series from biomonitoring schemes as a source of interaction data, (ii) network construction methods appropriate to these sources, (iii) how networks can be used to understand and mitigate insect declines.

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## Biomonitoring schemes as sources for interaction data

Despite some geographical skew, there are numerous systematic, long-term insect surveys around the world (van Klink *et al.*, 2020). The UK has a long history of insect monitoring and surveillance with notable examples including RIS, UKBMS, UK Environmental Change Network (ECN), and the Fera yellow water-pan trap network (YWP) among others. Typically, these biomonitoring schemes have specific purposes, such as monitoring plant pests (e.g. aphids) or bioindicators (e.g. moths, butterflies). For example, the RIS suction trap-network continuously traps aerial flying insects and the data are used to assess the population density and flight times of aphid species, which provides farmers with a risk forecast for certain crops. Crucially, this and many other biomonitoring schemes keep a wealth of 'non-target' insect community data, incidentally caught through routine sampling (RIS bycatch samples have been archived since 1974), which have enormous potential for constructing species-interaction networks across spatial and temporal scales.

Recent advances in molecular ecology, machine learning, big data, and network theory (e.g. Evans *et al.*, 2016, Bohan *et al.*, 2017) provide new opportunities for unlocking a more holistic understanding of the mechanisms driving insect declines. Before describing how insect surveys can be used to construct networks, we distinguish between two forms of insect survey datasets (see Fig. 1a, for graphical representation): 'physical' where biological samples are retained, taxonomically identified or not, and 'digital' where time series of insect samples are identified to some taxonomic level and stored electronically.

## Constructing ecological networks using insect survey data

There are three main, non-exclusive methods for constructing networks (Delmas *et al.*, 2019): (i) *literature searches* where trophic and/or other interactions are described; (ii) *observation* based on empirical study; and (iii) *predicting* species interactions from community data (Fig. 1b). The rapid growth and interest in network ecology in recent years has resulted in the proliferation of datasets around the world (e.g. Mangal https://mangal.io; Poisot *et al.*, 2016), often with a focus on bipartite interactions. Empirically derived networks are the result of painstaking observations of species-interactions in the field, but are increasingly being augmented using DNA-metabarcoding, especially to determine difficult-to-observe interactions (Evans & Kitson, 2020). Alongside these developments, network inference approaches are being applied to insect community data (e.g. to species lists generated using environmental DNA) whereby species-interactions are predicted based on co-occurrence (presence-absence) conditional probabilities (but see Blanchet *et al.*, 2020 for a critique).

Recent work by Redhead et al. (2018) provided a novel way of showing how multiple sources of biological recording data, that included citizen science records, were used to build nationwide plant-pollinator networks, and found positive relationships

between agricultural land cover and both pollinator generality (one of many network metrics) and robustness under several extinction scenarios. Building on this, combining network construction methods using long-term target and non-target insect biomonitoring scheme data represents a significant opportunity to understand the extinction dynamics of more holistic insect interaction networks.

## Network applications for insect biomonitoring schemes

Using the RIS 12.2 m suction-trap network as an exemplar, we show how biomonitoring schemes can be used to generate different types of network data, and, here we use the bycatch from the suction traps as a representative sample of the aerial community. These suction-traps are widely used in temperate systems around the world (18 countries, 128 sites) but other methods could prove equally productive in yielding a bycatch for study, such as YWP and Malaise traps, the latter of which is excellent for sampling insects in tropical systems (Skvarla et al., 2021). First, it is possible to use collected insect samples to look for direct interactions between species. For example, molecular methods can be used to screen ladybird gut contents for aphids (predator–prey interactions), and/or aphids (and non-target species) for symbionts and parasitoids (Fig. 1b; (ii)), with interaction data retained in bioinformatic pipelines that can then be used to construct networks (see Kitson *et al.*, 2019). Network data can then be used to examine long-term changes in species-interactions, in this case regarding questions of disease transmission and pest regulation. Second, the bycatch can be identified by metabarcoding the bulk sample, representing a more holistic community of interacting species when trapping allows (acknowledging in this instance the focus on aerial insects using a particular trapping method). Testing a range of co-occurrence algorithms on insect community data derived from metabarcoding is necessary (Fig. 1b; (iii)), but for RIS validation is easier as the interactions between agricultural insects are generally well documented. Third, networks can be constructed in space and time by scaling up the molecular processing of catches using automation, resulting in daily, weekly, and monthly insect networks at each suction trap across the country (acknowledging the need for validation (Piper *et al.*, 2019) and appropriate methods for obtaining insect abundance data (Ji *et al.*, 2020)). Importantly, there is an opportunity to construct historic networks by metabarcoding-stored insect sample archives, potentially non-destructively and assuming DNA degradation is not a hindrance. Long-term changes in network structure, complexity, interaction turnover, and robustness can then be examined in relation to environmental change, allowing new insights into the drivers of insect declines and the consequences for ecosystem functioning.

## Understanding insect declines: An ecological network approach

General reviews on the analysis, applications, and limitations of networks already exist (Delmas *et al.*, 2019). In the context of insect declines, however, we suggest the following directions for
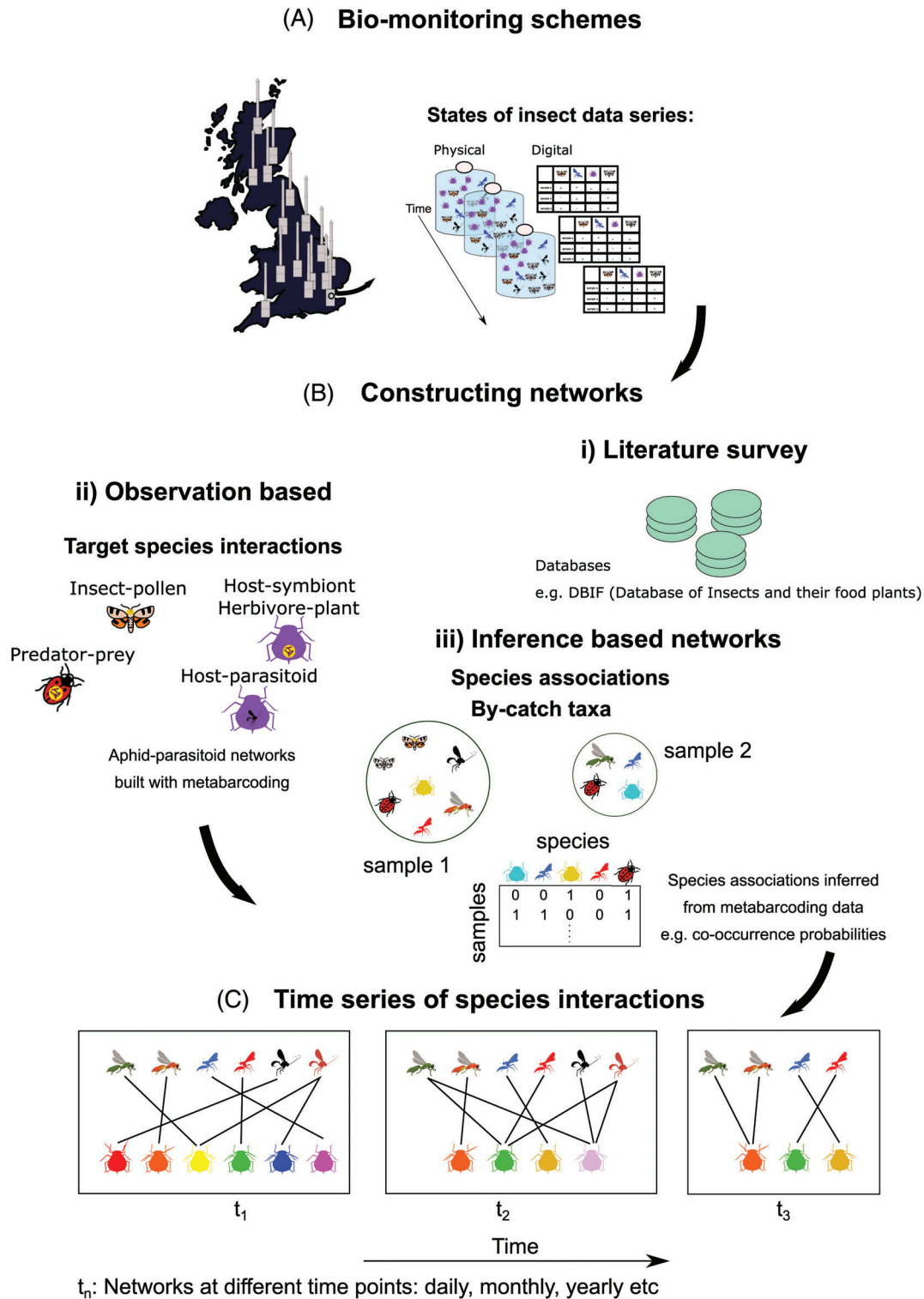
## (A)  **Bio-monitoring schemes**

**States of insect data series:**

Physical    Digital

Time

## (B)  **Constructing networks**

### i) Literature survey

Databases

e.g. DBIF (Database of Insects and their food plants)

### ii) Observation based

**Target species interactions**

Insect-pollen     Host-symbiont
Herbivore-plant

Predator-prey

Host-parasitoid

Aphid-parasitoid networks
built with metabarcoding

### iii) Inference based networks

**Species associations**
**By-catch taxa**

sample 2

sample 1

species

| | | | | |
|---|---|---|---|---|
| 0 | 0 | 1 | 0 | 1 |
| 1 | 1 | 0 | 0 | 1 |

samples

Species associations inferred
from metabarcoding data
e.g. co-occurrence probabilities

## (C)  **Time series of species interactions**

$t_1$          $t_2$          $t_3$

Time

$t_n$: Networks at different time points: daily, monthly, yearly etc

**Fig. 1.** (a) *Insect biomonitoring schemes* can have collections of insect data series which can be *physical* (archived samples) or *digital* (in databases). (b) *Constructing networks*: Constructing networks from such samples can be achieved from: (i) *literature* searches, databases etc.; (ii) *observation*, based on targeted interactions via metabarcoding e.g. host-parasitoids; (iii) From *inference*, where species associations are inferred based on co-occurrence. (c) Using different sources can result in time series of species interactions at different time scales (e.g. daily, weekly, yearly).
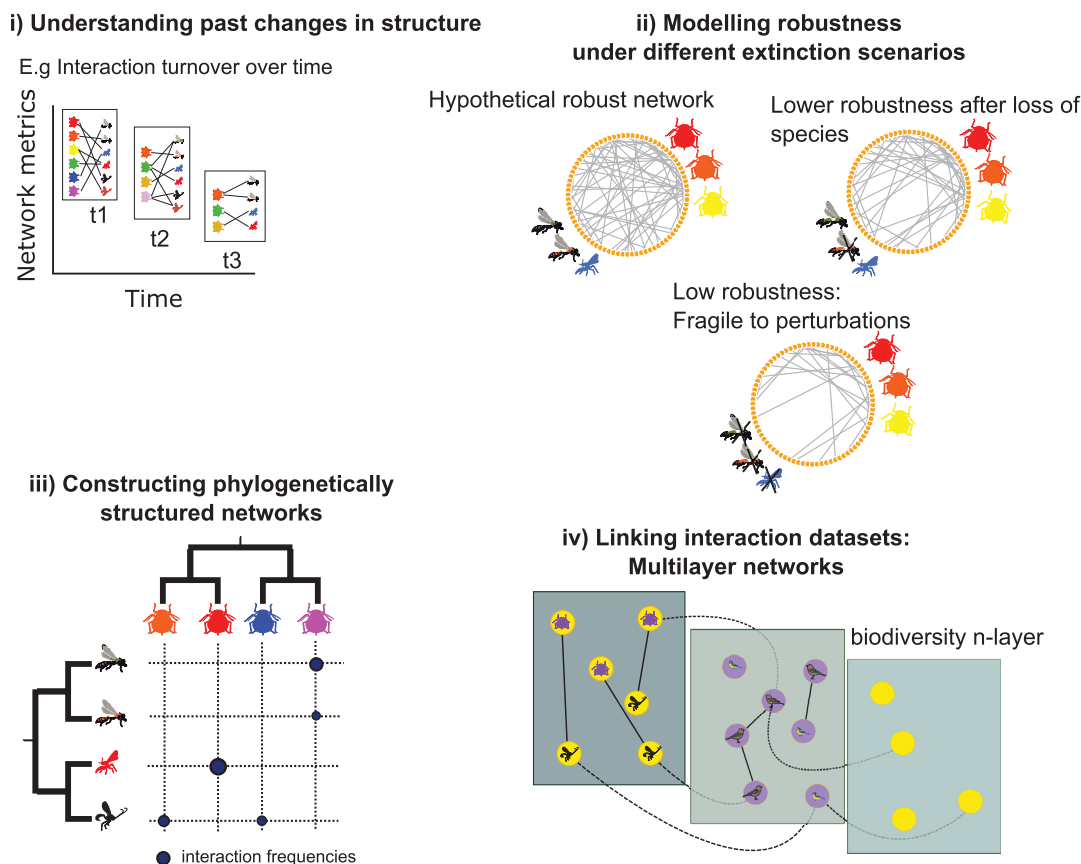
## Networks for bio-monitoring schemes:

### i) Understanding past changes in structure

E.g Interaction turnover over time



### ii) Modelling robustness under different extinction scenarios

Hypothetical robust network

Lower robustness after loss of species

Low robustness: Fragile to perturbations



### iii) Constructing phylogenetically structured networks



interaction frequencies

### iv) Linking interaction datasets: Multilayer networks

biodiversity n-layer



**Fig. 2.** *Networks for biomonitoring schemes*: Having constructed such networks we highlight four possible uses: (i) *Understanding past changes* in structure by analysing network metrics through time; (ii) *Modelling robustness* under extinction scenarios; (iii) *Construct phylogenetically structured networks* to examine eco-evolutionary dynamics; (iv) Linking interaction datasets with *multilayer networks* e.g. insect interactions with birds or bats.

further research (see Fig. 2). First, the construction of insect networks using 'physical' and 'digital' long-term datasets can be applied to multiple types of insect monitoring schemes around the world (and well beyond those highlighted here). Some additional examples include The Global Malaise Trap Program (http://biodiversitygenomics.net/projects/gmp/) and global volunteer insect monitoring initiatives (see Bried *et al.*, 2020). For a more comprehensive list of long-term insect time series and their associative monitoring schemes see Table S1 in van Klink et al. (2020) and Dornelas et al. (2018). This can provide new opportunities to examine whether network structure, complexity, and interaction turnover has changed over time and across large spatial scales, while identifying the key drivers. Bohan et al. (2017) show how next-generation sequencing data combined with machine-learning could be combined in future global biomonitoring schemes, through autonomous samplers deployed over large geographical areas. This could construct highly replicated networks of ecological interactions, allowing potential changes in ecosystem function to be observed for the first time. Second, examining the robustness of networks to species extinctions shows promise (see Kehoe *et al.* 2020

regarding extinction cascades as a driver of insect decline). For mitigation purposes, it not only has the potential to identify 'fragile' insect groups, but also species which are disproportionately important for the integrity of the network which could be targeted for conservation management. For example, Pocock et al. (2012) identified insect pollinator networks as most vulnerable to species loss on farmland compared to the other animal groups studied. At the farm scale, their analysis identified common agricultural plants such as clovers (*Trifolium* spp.), thistles (*Cirsium* spp.), and buttercups (*Ranunculus* spp.) that theoretically could be managed to increase robustness and improve overall agroecosystem resilience. Similarly, Evans et al. (2013) showed how habitat robustness analyses could be used to identify key agricultural habitats for targeted management to increase resilience, in this case hedgerows and waste ground, which together comprised <5% of the total farm area. Scaling up further, Redhead et al. (2018) showed how network robustness analyses can also be used to identify key species traits that enable persistence in highly perturbed landscapes. Thus, robustness measures could be used in ecosystem restoration to boost the resilience of insect communities,

although this is yet to be tested empirically. Third, the use of DNA-metabarcoding (and in the future metagenomics (Cordier *et al.*, 2020)) to construct phylogenetically structured networks is a research priority (Raimundo *et al.*, 2018). Currently, the use of adaptive network models for predicting ecological restoration outcomes shows considerable promise but are severely hampered by the lack of long-term species-interaction data. We contend that this could quickly be overcome by making use of long-term biomonitoring insect archive samples, such as RIS. Finally, recent advances have started to pull together different network types into multilayer networks (Pilosof *et al.*, 2017). This presents a new way of examining the implications of insect declines on a large array of other taxa that interact with them (e.g. birds and bats), providing new ways to examine how the loss of some insect groups leads to further insect extinctions.

## Acknowledgements

## Data availability statement

Data sharing not applicable to this article as no datasets were generated or analysed during the current study

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