


# Interpreting insect declines: seven challenges and a way forward

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**Abstract.** 1. Many insect species are under threat from the anthropogenic drivers of global change. There have been numerous well-documented examples of insect population declines and extinctions in the scientific literature, but recent weaker studies making extreme claims of a global crisis have drawn widespread media coverage and brought unprecedented public attention. This spotlight might be a double-edged sword if the veracity of alarmist insect decline statements do not stand up to close scrutiny.

2. We identify seven key challenges in drawing robust inference about insect population declines: establishment of the historical baseline, representativeness of site selection, robustness of time series trend estimation, mitigation of detection bias effects, and ability to account for potential artefacts of density dependence, phenological shifts and scale-dependence in extrapolation from sample abundance to population-level inference.

3. Insect population fluctuations are complex. Greater care is needed when evaluating evidence for population trends and in identifying drivers of those trends. We present guidelines for best-practise approaches that avoid methodological errors, mitigate potential biases and produce more robust analyses of time series trends.

4. Despite many existing challenges and pitfalls, we present a forward-looking prospectus for the future of insect population monitoring, highlighting opportunities for more creative exploitation of existing baseline data, technological advances in sampling and novel computational approaches. Entomologists cannot tackle these challenges alone, and it is only through collaboration with citizen scientists, other research scientists in many

disciplines, and data analysts that the next generation of researchers will bridge the gap between little bugs and big data.

**Key words.** Citizen science, detection bias, global insect decline, insect conservation, monitoring, phenological shift, population trend, sampling bias, shifting baseline, time series.

## Introduction

Populations of many insect species are declining (Wagner, 2020). For the vanishingly small proportion of these in which conservation risk has been evaluated (e.g. Langor, 2019), the status and trends are at least as sobering as they are for vertebrate species (Dirzo *et al.*, 2014; Forister *et al.*, 2019). This will, of course, come as no surprise to entomologists, who have been reading about declining insect populations in *Insect Conservation and Diversity*, among other journals, for at least a decade (e.g. Shortall *et al.*, 2009; Fox, 2013; Cardoso & Leather, 2019). For the general public, however, it has come as an alarming revelation, brought to the fore by several recent studies that received worldwide media attention (e.g. Hallmann *et al.*, 2017; Lister & Garcia, 2018; Sánchez-Bayo & Wyckhuys, 2019). The quality of some of these papers has been relatively weak, either due to misinterpretation of data (Lister & Garcia, 2018) or due to overzealous claims (Sánchez-Bayo & Wyckhuys, 2019). The scientific response to this has been an exemplar of the nature of science as a self-correcting endeavour, with critical re-evaluation of the findings emerging rapidly (e.g. Willig *et al.*, 2019; Cardoso & Leather, 2019; Cardoso *et al.*, 2019; Komonen *et al.*, 2019; Montgomery *et al.*, 2020; Mupepele *et al.*, 2019; Simmons *et al.*, 2019; Thomas *et al.*, 2019; Wagner, 2019; Saunders *et al.*, 2020a). The global media response has been something entirely different but has put insect conservation firmly on the public and policy agenda (Harvey *et al.*, 2020). As Cardoso *et al.* (2019) and Montgomery *et al.* (2020) point out, though, this spotlight could become a double-edged sword as the veracity of the more alarmist ‘insect decline’ statements faces increased scrutiny.

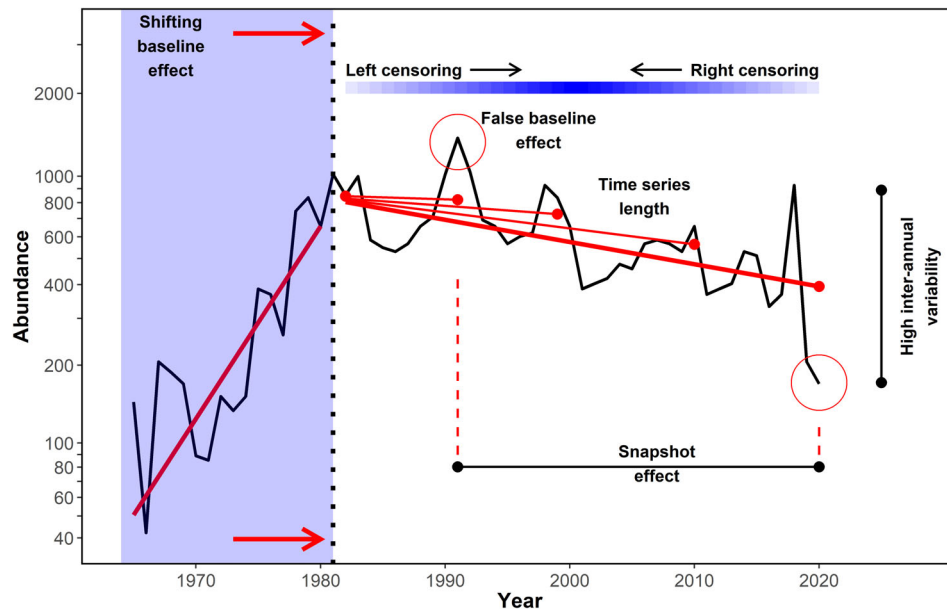
In the rush to address ‘global insect declines’, it has never been more important to pause and think critically about what constitutes evidence for decline in the first place. For most insects, high inter-annual variability is the norm rather than the exception (e.g. Redfearn & Pimm, 1988; Roubik, 2001), but it poses serious problems in determining what the baseline reference state should be for historical abundance, and inherently increases the length of time series required to separate signal from noise (White, 2019). Any number of artefacts in the data compilation, analysis or interpretation of the findings could also result in an apparent change from presence to absence or high-to-low abundance between two time points, without there necessarily being a significant trajectory of decline in population size through time. Here, we identify seven key problems in quantitative inference about insect declines, grouped loosely as errors of baseline, trend estimation and resulting population inference. This is not intended to be a comprehensive review of the subject but rather a framework for approaching the broad and growing

literature on insect population trends through time, with selected examples to illustrate key challenges in inferring a decline in abundance. The seven problems we identify are not intended to be mutually exclusive either, and there will be substantial conceptual overlap in how they are dealt with and resolved. We conclude by presenting guidelines for best-practise approaches to mitigate bias, and a forward-looking prospectus for the future of insect monitoring, aimed at an up-and-coming generation of researchers who can bridge the gap between little bugs and big data.

### *The false baseline effect*

One logical precondition for estimating rates of long-term population decline is to have a sound quantitative estimate of historical population abundance. Frustratingly, such estimates are rarely available, as the vast majority of ‘decline’ studies only begin after numbers were perceived to be changing (Bonebrake *et al.*, 2010); a similar picture is seen with pest insects, where studies are typically only started in response to outbreaks (Watt & Hicks, 2000; Hicks *et al.*, 2008). At face value, this might suggest that current decline estimates should, on average, be underestimates of the longer-term trends (for instance, saproxylic insects, such as *Rhysodes sulcatus* Fabricius 1787, are thought to have been declining across Europe for the past 3000 years due to progressive loss of old-growth forests; Speight, 1989). We suspect that measured baselines might generally underestimate true historical baselines (e.g. Powney *et al.*, 2019), but speculative backcasting from the sorts of declines found by Hallmann *et al.* (2017) and others (e.g. 75% decline in insect biomass since the 1980s), could be problematic from the outset. For example, Macgregor *et al.* (2019) found that the period from the 1980s to present was indeed a period of declining moth biomass in the United Kingdom, but the data from an even earlier baseline period (1967–1982) showed that moth biomass was previously much lower than at present and had actually increased to a peak in the 1980s (for unknown reasons) prior to the more recent decline. This is a clear example of the well-known *shifting baseline* phenomenon (Soga & Gaston, 2018), in which perception of the reference state is dependent on how comprehensive our historical knowledge is of former conditions (Fig. 1).

In the absence of long time series of decline, many studies use a haphazard assortment of historical data as proxies for the missing baseline (Bonebrake *et al.*, 2010), but despite these often being all that we have, they are rarely likely to be fit for purpose. For instance, historical quantitative surveys might have been designed to address an unrelated ecological question and there-



**Fig. 1.** Schematic representation of some of the potential pitfalls in quantitative estimation of population change through time. The trend line is a hypothetical (not empirical) time series of insect abundance values over 55 years, loosely based on the form of the trend line for moth biomass change in the United Kingdom in the study by Macgregor *et al.* (2019). Without good knowledge of historical conditions, perception of changes through time can be strongly biased by shifting baseline effects. Moreover, any non-random bias towards an above-average starting point in a time series comparison could lead to a false baseline effect. This might be particularly problematic in simple pairwise snapshot effects if there is also bias in the selection of the contemporary time-point for comparison. These kinds of effects are likely to be most severe when inter-variability in abundance is high. Longer time series will increase the signal to noise ratio and statistical power. Cross-validation approaches, such as left-censoring and/or right-censoring time series, have been suggested to test the sensitivity of trends to underlying bias in the data. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

fore (inadvertently) violate the statistical assumptions needed to produce an unbiased estimate of historical population abundance. Using data simulations, Fournier *et al.* (2019) describe how non-random site selection bias in the measurement of historical baseline conditions could significantly increase the probability of inferring a false decline, even when there is no long-term trend in the data. This (they argue) is because researchers are much more likely to select sites where their study organisms are known to occur and/or are sufficiently abundant to sample. Plausibly, an above-average starting point in a time series comparison – a *false baseline effect* (Fig. 1) – could lead to an apparent decline through time as a simple statistical artefact of regression to the mean, especially when abundances are fluctuating widely from year to year (Fournier *et al.*, 2019).

In practise, errors of baseline estimation almost certainly have components of both shifting baseline effects (historical abundance is assumed to be accurately estimated, but there is no knowledge of trends leading up to that point in time) and false baseline effects (the appropriate reference window is known, but historical abundance is inaccurately estimated).

#### *The missing zero effect*

The corollary of site-selection bias inflating average local abundance at baseline is that unoccupied sites (i.e. true absences, not detection errors) will be under-represented in local population estimates. Assuming that these unoccupied sites are

potentially occupiable (i.e. represent suitable habitat, linked by dispersal, in some sort of spatially structured population context; Hanski, 1998; Ovaskainen & Saastamoinen, 2018), then rates of decline will be over-estimated at the local sites where abundances are measured, and unrepresentative of the wider sampling universe of potentially occupiable habitat. We call this the *missing zero effect*, after the wonderful children's mathematics book *Nesta and the Missing Zero* (Leibrich, 2006) in which the loss of 'nothing' throws the world into chaos. Local populations might well be declining at known sites with high historical abundance, but other local populations could be increasing (concurrently) at formerly unoccupied or unsampled sites, especially if there are density-dependent feedbacks on intrinsic rates of population increase or asynchronous dynamics among local subpopulations (Pollard, 1991; Sutcliffe *et al.*, 1996).

At local scales, the missing zero effect squanders the opportunity to measure future recolonisation of unoccupied sites, through (i) natural processes associated with spatially structured population dynamics (Ovaskainen & Saastamoinen, 2018; Dallas *et al.*, 2020), (ii) rehabilitation of sites following mitigation of threatening processes (e.g. Corlett, 2016; Pilotto *et al.*, 2018), or (iii) as a result of extra-limital processes such as shifting geographic ranges due to climate change and species invasion (e.g. Walther *et al.*, 2009; Hill *et al.*, 2012; Hill *et al.*, 2017; Rabl *et al.*, 2017). At the regional scale, missing zeros are also the connection between local abundance measures and regional occupancy changes, with which we deal separately below.

### *The snapshot effect*

Estimates of population change can be sensitive to selection bias effects in the choice of contemporary time-points, much as described for false baseline effects above. In the simplest case (i.e. a pairwise *snapshot* comparison of historical versus contemporary populations; Fig. 1), there is high potential for time-selection bias in contemporary estimates. Anecdotal reminiscing about how ‘numbers are not what they used to be’ (e.g. Vogel, 2017) could easily lead to confirmation bias in the choice of a single contemporary time-point where numbers are substantially lower than average contemporary conditions (e.g. Fig. 1). The motivation for selecting a particular time-point for comparison and knowledge of fluctuations in the intervening years are fundamentally important considerations in evaluating snapshot data (viz criticisms about the Lister & Garcia, 2018 study).

Pairwise point estimates of local population change should be treated for what they really are – a time series of two points. Such paired comparisons have been used effectively for comparing differences in occupancy through time (e.g. climate-driven range expansions), but they are unavoidably weak when the focal variable is abundance. It is not inconceivable that such a limited time series could have sufficient statistical power to detect a difference in abundance, but the likelihood is very low unless the degree of spatial replication is very high. For example, LeBuhn *et al.* (2013) concluded that 200–300 sites, each sampled twice at an interval of 5 years, would be needed to detect 1–2% annual change in the abundance or richness of insect pollinators across a region. At single sites, although, White (2019) showed that at least 15 time points are required to have sufficient statistical power to detect non-random trends in abundance through time, with shorter time series only having sufficient power when the trend slope is unusually steep and inter-annual variability in abundance unusually low (*cf.* Fig. 1). This combination of characteristics is likely to be both rare (particularly for insects) and difficult to validate, so the more parsimonious explanation is inherently going to hold sway; i.e., that the apparent slope of the trend line is simply an artefact of the narrow window (or low frequency) of observations (Fig. 1). For example, the conclusions of a long-term study of pollination services in Colorado, USA, changed from a ‘significant decline’ when studied over a moderate time series (11 time points over a 17-year period from 1993 to 2009; Thomson, 2010) to ‘no decline’ over a longer time series (20 time points over 26 years from 1993 to 2018; Thomson, 2019). More generally, Fox *et al.* (2018) showed that IUCN Red List assessments based on time series of only 10 time points were unacceptably biased by stochastic artefacts of the sampling window.

Fournier *et al.* (2019) suggest that left-censoring of time series (Fig. 1) can be a useful approach to detect and overcome potential false baseline effects (effectively a sensitivity test of whether the trend slope remains unchanged with progressive removal of early time points in the time series). They found that false baseline effects over-estimated decline slopes most substantially in time series with fewer than 10 time points (Fournier *et al.*, 2019). The same logic could potentially be used for right-censoring short-time series to overcome bias in contemporary snapshot effects (Fig. 1). Framing the combination of the two

approaches more generally, a walk-forward cross-validation or combinatorial k-fold cross-validation procedure for time series (e.g. Bergmeir *et al.*, 2018) could be used to determine sensitivity to outliers in the data, when time series are shorter than the 15 time points recommended by White (2019).

A salient example of just how important cross-validation could be is the recent study of arthropod decline in Germany over a 10-year time series from 2008 to 2017 (Seibold *et al.*, 2019). The overall time series trend, as well as region-specific and taxon-specific trends, are heavily influenced by one or two time-points in the data (see Fig. 1 and fig. S3-1 in the study by Seibold *et al.*, 2019). To their credit, the authors attempt a sensitivity analysis by dropping 1 year of the time series at a time, which “showed that the decline was influenced by, but not solely dependent on, high numbers of arthropods in 2008” (Seibold *et al.*, 2019, p. 672). This is equivalent to a very shallow left-censoring of the time series in the case of the 2008 data point, which (by visual inspection of the evidence in the study by Seibold *et al.*, 2019) will have removed a large component of the apparent trends, by itself alone. A full cross-validation would certainly nullify any remaining evidence for a general decline trend in their data. This is not to say that such a decline in arthropods is not occurring in these parts of Germany. The decline may well be real, but at face value, the data provide no indication whether abundance in the next time-interval will be lower or higher than current estimates – and what is a time series of decline for, if not to improve predictive power to understand future population change?

### *The detection bias effect*

All the arguments presented so far have assumed that variation in sample abundance is an accurate representation of variation in local population abundance. Unfortunately, few studies can achieve a complete census of all individuals in a population, so it is a practical necessity in insect monitoring that standardised sampling methods are used instead. Entomologists are well aware that most sampling methods measure activity rates not population abundance, all methods have inherent biases, and different methods have different biases that affect the accuracy of extrapolation to local abundance or population size estimates (e.g. pitfall trapping: Baars, 1979; or pollinator monitoring: Westphal *et al.*, 2008). Such biases are not necessarily problematic if their effects are randomly distributed with respect to the spatial and temporal trends of interest. There are, however, a number of potential processes that could result in temporal autocorrelation in the detectability of individuals, such that abundance might appear to change through time simply because individuals are becoming more or less detectable. It is this potential for temporal autocorrelation in detectability that needs closer investigation. Here, we provide only a partial (and cursory) set of examples of detection bias (for further examples, see Isaac & Pocock, 2015), and there are likely to be many other situations in which temporal autocorrelation in detectability might occur (setting aside the apocryphal *car windscreen design effect*, in which declining insect splatter rates on cars could be due solely to the design of more aerodynamic modern cars; Vogel, 2017).

A *detection effect* might operate if the ability to capture or census individuals changes with ambient environmental conditions (regardless of their actual abundance). The most obvious example of this is that insect activity rates (and therefore probability of detection) depend on ambient weather conditions (which are also changing through time). Detection can also change with increasing human alteration of other aspects of environmental conditions, such as artificial lighting at night. One way to monitor populations of the glow-worm, *Lampyrus noctiluca* (Linnaeus, 1767) (Coleoptera: Lampyridae) is by counting the numbers of glowing females per km of transect (Gardiner, 2007; Gardiner & Didham, 2020), but an increase in the intensity, or a change in the spectrum, of ambient background lighting through time (from street lights, for instance) could make it increasingly difficult to detect females, even when present. This is further complicated by the possibility that male glow-worms have difficulty finding females against artificial background lighting, which could produce real population-level consequences over the longer term (Owens *et al.*, 2020; A. Stewart, pers. obs).

Plausibly, in attraction-based trapping, a *dilution effect* could occur if an attractive stimulus from competing anthropogenic sources was itself increasing through time. For example, light trapping is used as a standard method for sampling moths, but in many rapidly urbanising areas, the number of competing anthropogenic sources of light has been increasing dramatically through time (Gaston *et al.*, 2015; Owens *et al.*, 2020). Thus, moth captures might decline through time simply because individuals are attracted elsewhere and are not as detectable in the monitoring traps. In principle, this is no different than the well-known phenomenon that light traps catch more moths on dark moonless nights than during the full moon, as a result of less competition from other light sources (McGeachie, 1989). There might be a tendency to think of this as just an urban problem, but dilution effects could affect populations far from urban centres if artificial lighting affects regional dispersal. Such effects are not known for artificial lighting, but in agroecosystems, landscape-scale dilution effects from mass-flowering crops have caused reductions in the local capture rate of pollinators (Holzschuh *et al.*, 2011), without necessarily changing regional population size. Naturally, the converse *concentration effects* from attraction-based trapping could plausibly occur as well, if there is temporal covariance between lower ambient resource attraction in the environment and consequent increased attraction to the baited trap, even if local population size does not change (for instance, in baited pitfall trapping for dung beetles during years of low dung availability, pheromone trapping for bark beetles when attractive volatile signals from host trees are low, or coloured pan trapping for bees during years of floral scarcity; e.g., Baum & Wallen, 2011).

If artificial stimulus effects, such as attraction to light, are also compounded by an added component of source-sink dynamics in the potential mortality associated with the stimulus, then this could be a driver of real declines in abundance, over and above dilution effects (Minnaar *et al.*, 2015). For instance, mortality is thought to be substantially higher for some species in artificially lit areas (e.g. where bat predation on moths is focused around streetlamps; Owens *et al.*, 2020), imposing an extreme selection pressure on some local populations. Ironically, this

*selection effect* could also make evolving moths harder and harder to detect through time in light-trap monitoring surveys. For example, Altermatt & Ebert (2016) reared *Yponomeuta cagnagella* (Hübner, 1813) moths from populations in light-polluted versus dark-sky regions of France and Switzerland and found that moths from high light pollution areas had a significant (30%) reduction in flight-to-light behaviour. This type of selection effect could result in an overestimate of apparent declines in population size, due to increasing trap shyness through time.

Finally, apparent local declines in abundance could occur due to a *depletion effect* from removal sampling (e.g. kill-trapping of insects) in species that have low intrinsic rates of population increase and very low dispersal ability (e.g. large-bodied, flightless Carabidae beetle species in pitfall trap sampling programmes; Ward *et al.*, 2001). The declines themselves are real at the local level but driven by the monitoring programme and not other ecological causes that the monitoring programme was designed to test. We stress that it is unlikely for standardised quantitative monitoring programmes to cause population-wide decline due to over-collection (e.g. Gezon *et al.*, 2015), although the potential risks to rare or localised species should always be evaluated carefully. In the sense that local depletion effects are unrepresentative of wider regional population changes, then this is a detection bias issue that arises due to low recruitment rates into the sampled population prior to the next sampling interval.

#### *The Andrewartha effect*

When baseline identification, site selection, trend estimation, and detectability are all known to be unbiased, the natural temptation might be to infer that sample estimates of decline equate directly to the real magnitude of population decline. Yet, there are several reasons why caution is still needed in drawing population-level inference.

The first reason is that many insect decline studies are founded on an implicit, but untested, assumption that insect dispersal rates are density independent. Many (perhaps most) insect monitoring methods are based on detecting moving insects, such as beetles in pitfall traps, wasps and flies in Malaise traps, or aphids in suction traps. Logically this means that changes in sample abundance are only a good proxy for changes in population abundance if activity rates are density independent. The problem is that at high population densities, the frequency of dispersal events might be expected to increase in a density-dependent manner (e.g. due to local resource limitation), while at lower population densities, the frequency of dispersal events might be expected to decline and not necessarily in a linear manner (Denno & Peterson 1995; Enfjäll & Leimar, 2005; Régnière & Nealis, 2019). If this is generally the case, then movement-based monitoring techniques might overestimate population size at peak abundance, and underestimate population size in population troughs, potentially resulting in over-estimates of rates of decline as populations get smaller (as well as the converse, as populations get larger). In rarer cases, the opposite pattern of negative density dependence in dispersal rates has also been shown in some damselfly species with unusual habitat requirements (Chaput-Bardy *et al.*, 2010), or where conspecifics are

potentially used as cues for habitat quality (Roquette & Thompson, 2007). In all of these cases, density dependence in insect movement rates is incompatible with a direct extrapolation from declining sample abundance to declining population size. We call this the *Andrewartha effect* after the renowned Australian ecologist H.G. Andrewartha for whom density dependence was pure dogma, and all population processes were implicitly assumed to have a density-independent basis until proven otherwise (Andrewartha, 1961).

#### *The groundhog effect*

A second potential problem in population-level inference is that sample abundances might falsely indicate a decline in population size through time because of a progressive phenological shift in insect activity in response to changing climate, or other environmental factors (Parmesan & Yohe, 2003; Cohen *et al.*, 2018). We call this the *groundhog effect* because annual monitoring dates cannot simply be treated as ‘groundhog day’ for re-sampling each year across long time series, due to the very real possibility of phenological mismatch between sampling and activity periods through time. The extent of this effect is difficult to gauge but will be most severe where monitoring windows were historically very narrow, and where the activity of target species is known to be sensitive to seasonal variation in environmental conditions (increasing the probability of peak seasonal abundances falling progressively further outside the monitoring period). Certainly, in recent studies, shifting phenological responses of species through time have been shown to explain significant variation in models of insect decline (Møller, 2019; Gardiner & Didham, 2020). The issue of shifting seasonal phenology clearly suggests that a fixed calendar-based sampling approach can be inappropriate in some circumstances (as recognised in the pest management literature, where a degree-days approach is used), unless monitoring fully brackets the phenological window and models adjust for inconsistency of environmental responses through time (Gardiner & Didham, 2020).

#### *The popcorn effect*

A final potential problem in population-level inference is validating the extent to which a small set of well measured local decline estimates can be extrapolated to reduction in local and regional abundance patterns that might ultimately lead to population extinction (in the extreme). In other words, the degree of covariance between local and regional estimates of population change is typically unknown (but see Oliver *et al.*, 2017). There is a tendency to take a few kernels of local data and expand these into a superficially inflated shell of population response as a whole. In consumer psychology, the *popcorn effect* is where a new phenomenon pops into a person’s mind and then that same phenomenon appears to pop up everywhere, in a form of unconscious bias, as if it is a generalised truth (also known as the frequency illusion effect, or Baader-Meinhof phenomenon). In the context of population change, the popcorn effect could result in

misleading conclusions if there are substantial gaps in sample coverage of occupied versus unoccupied areas (e.g. the *missing zero effect* referred to above), such that local declines are not representative of changes in either occupancy or average abundance across the region.

The correspondence between local decline estimates and regional occupancy trends probably depends on the commonness or rarity of species sampled. From first principles, very large local declines in aggregate measures of insect abundance, and to a certain extent biomass (e.g. Hallmann *et al.*, 2017, 2020), must be driven predominantly by changes in the abundance of common, rather than rare species (Shortall *et al.*, 2009). Thus, statistical support for the local decline in abundance of common species is unlikely to correspond directly to a decline in range-wide occupancy or increased risk of extinction (barring a few celebrated examples, such as the extinction of the super-abundant Rocky Mountain locust *Melanoplus spretus* Walsh, 1866, Orthoptera: Acrididae, Lockwood, 2010). In contrast, it would be much more challenging to statistically prove local declines in any of the rare species in the aggregate samples. Yet in a comprehensive analysis of occupancy trends for 353 wild bee and hoverfly species in Great Britain from 1980 to 2013, Powney *et al.* (2019) showed that it was precisely these rarer species that declined the most in occupancy through time. There is of course the added complication that many occupancy studies, such as this, use relative measures of population change (e.g. inferring absences from the presences of other species in the same taxon). Equating relative population estimates to absolute population changes is not necessarily straightforward (for instance, if all species are declining then such methods might fail to detect declines even though they are happening).

Both occupancy and abundance trends provide unique, and complementary, evidence of declines, particularly if one is interested in the ecological or management implications of population declines (Wepprich *et al.*, 2019). As Powney *et al.* (2019, p. 3) state, “the lack of standardized monitoring data limits our understanding of the link between change in species occupancy, local abundance and [functional significance]” (pollination in their case). While rare species can be of great conservation significance, they might tend to have relatively little functional significance (in terms of contribution to ecosystem services such as pollination, pest control and so on), compared with abundant species (e.g., Winfree *et al.*, 2015; but see Dee *et al.*, 2019). Different management goals can require very different types of data and different requirements in terms of designing robust monitoring programmes (e.g. for pollination systems *cf.* LeBuhn *et al.*, 2013; Gallant *et al.*, 2014; Bartholomé & Lavorel, 2019).

### **A way forward**

Taken together, the seven potential challenges we have identified in accurately quantifying time series trends in insect populations suggest that much greater care is needed in evaluating the evidence for (and relative drivers of) declines. Equally, going forward, a number of key recommendations will be important to consider in monitoring prospective time series of recovery in

insect populations following mitigation of threatening processes (Harvey *et al.*, 2020).

- 1 **Baseline estimation:** Studies should explicitly state the limits to inference on their selected historical reference state, in terms of time frame, representativeness of expected past conditions, and the intrinsic magnitude of inter-annual fluctuations in population abundance of the target species (as this determines the precision, accuracy and reliability of forecasting and backcasting). More than one reference site (preferably many) should be sampled to determine baseline conditions, when possible. Studies should consider site selection bias when choosing these reference sites, with the aim of minimising or mitigating non-random selection (including consideration of unoccupied, but potentially occupiable sites), and in all cases should report site selection criteria in subsequent publications (Fournier *et al.*, 2019). Where multiple data types and approaches are used to establish baselines, the criteria for inclusion and integration should be transparent (Bonebrake *et al.*, 2010)
- 2 **Trend estimation:** Under most circumstances, time series snapshot comparisons between two time-points do not accurately reflect local abundance trends through time. At best, these will only show a statistical difference between 2 years sampled. Where these pairwise snapshots could gain value in the future, however, is in the integration of many such pairwise estimates at many sites over many time intervals to build a composite time series of evidence. For more robust direct measurements of population change, longer time series will be needed. The minimum required length of time series depends on the magnitude of temporal fluctuations in abundance (a signal-to-noise ratio issue), and we follow Fournier *et al.* (2019) in suggesting that sampling artefacts in trend estimation decrease in time series with more than 10 time-points, and White (2019) in suggesting that statistical power increases in time series with more than 15 time-points. Cross-validation procedures (left-censoring, leave-one-out cross validation against values with high leverage, and so on) effectively determine sensitivity of the overall trend to outliers in the data. We also encourage monitoring studies to standardise their presentation of population change estimates (standardised effect sizes for rates of change per annum, through time) and lay their predictive cards on the table by publishing forecast estimates in advance for the following year(s), then testing the accuracy of the observed vs. predicted population trajectories. Finally, given the intense demands on resources to support robust quantitative evaluation of population trajectories, even at a relatively limited number of sampling locations, we recommend that intensive monitoring programmes (typically 10–100 sites) conducted annually (e.g. Karlsson *et al.*, 2020) are complemented by spatially extensive occupancy surveys (e.g. 100–1000 sites) at less frequent intervals (e.g. every 3–5 years) perhaps using citizen science programmes if data quality can be assured. The statistical bar for accurate, precise and reliable estimation of regionwide occupancy trends through time will be substantially lower (for most taxa) than

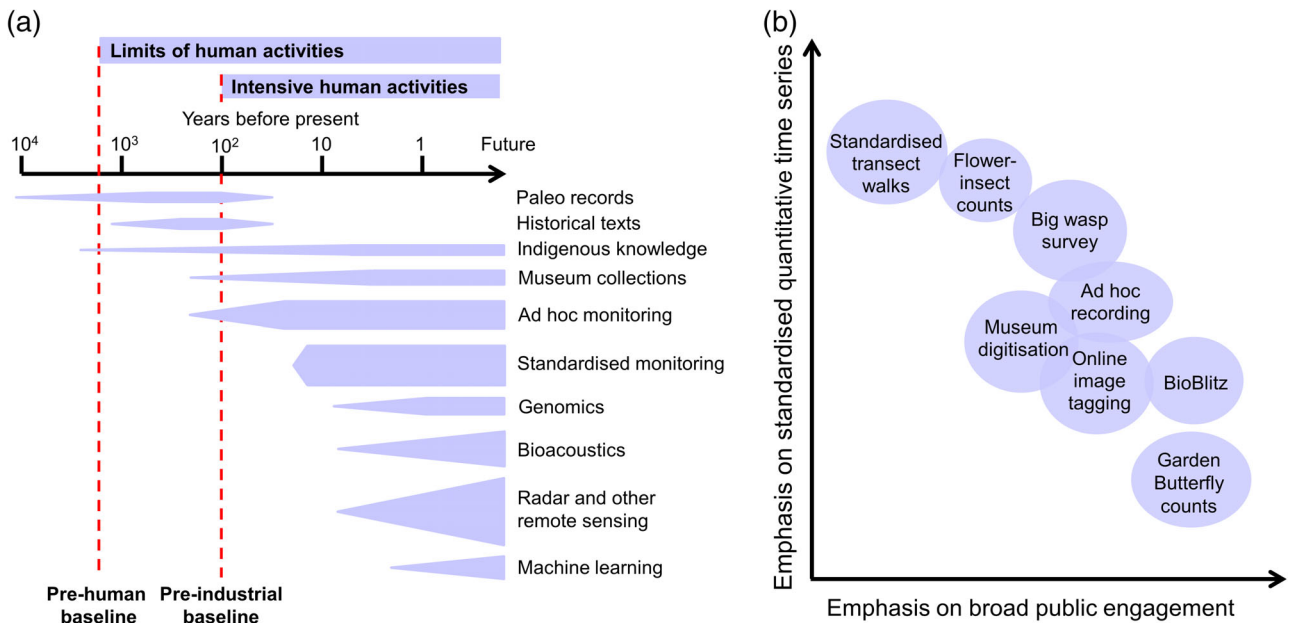
it is for quantitative local abundance trends, making occupancy data the logical target for citizen science monitoring.

- 3 **Population inference:** Studies using sampling methods in which the probability of capture of each individual is not uniform through time (which applies to essentially all quantitative insect sampling methods), should consider (and ideally test and report, where possible) the effects of relevant detection bias effects, density-dependent variation in capture probability, temporal covariance in the match between sampling period and insect activity period, and the degree of covariance between local detection frequency and wider landscape-level occupancy patterns and regional population size.

At this time, there is no way of quantifying the magnitude of the collective bias that the seven issues identified here might create in insect time series data, or whether published decline estimates are typically under-estimates or over-estimates of true population change without conducting a formal meta-analysis across studies (using standardised metrics, which are not readily available). Subjectively, the examples presented above suggest to us that most biases will lead to over-estimates of reported rates of insect decline, particularly for the false baseline effect, the snapshot effect (and other published decline estimates from very short time series), the missing zero effect, most of the detection bias effects, and most inferences from sample-level to population-level statistics (the Andrewartha effect, groundhog effect and popcorn effect). The exception (in our subjective opinion, once again) could be the shifting baseline effect, in that current population trend estimates might underestimate the magnitude and rate of losses that would have been inferred if we had older and more reliable historical baseline estimates – simply because of the massive scale and intensification of anthropogenic impacts on insect populations that had already occurred prior to quantitative baseline monitoring. Converse examples of lower baseline levels in earlier time intervals, such as those found for moth biomass in the United Kingdom by Macgregor *et al.* (2019), and emulated here in Figure 1, serve as a useful foil for the general conceptual problem of shifting baselines but may be the exception rather than the norm (in our opinion).

Despite many existing challenges and pitfalls, opportunities for creative exploitation of existing baseline data (Bonebrake *et al.*, 2010; Habel *et al.*, 2019; Stepanian *et al.*, 2020) and novel computational approaches (e.g. Outhwaite *et al.*, 2018) may resolve some issues. Drawing inspiration from climate science, which has sought to describe trends and attribute drivers in much the same way, researchers could attempt to cross-validate proxies for insect abundance and diversity in overlapping time periods to create a coherent time series (Fig. 2a). Tools for measuring population variation over time and accounting for complex ecological information (Saunders *et al.*, 2019; Bahlai & Zipkin, 2020) already exist in different fields such as paleoecology (e.g. Wilf *et al.*, 2001; Howard *et al.*, 2009), and conservation genomics (Beichman *et al.*, 2018). Other emerging approaches, like using machine learning to reverse-engineer the drivers of decline from empirical trends, may dramatically improve analysis and interpretation (Martin *et al.*, 2018). The





**Fig. 2.** The range of complementary data sets that feed into entomological monitoring initiatives. (a) Data sets tend not to cover the most important period of monitoring: the time before substantial human impact. Attempts to integrate across these data sources have been minimal but are essential to understand older patterns and establish baselines. (b) The goals of citizen science monitoring programmes vary on a continuum ranging from high emphasis on broad public engagement and education (e.g. for species that are easily identified, such as butterflies in backyard garden counts, or where substantial expert assistance can be delivered at specific times, such as in a BioBlitz), through to a higher emphasis on the collection of standardised quantitative time series data (e.g. for recording changes in regional occupancy patterns through time, or standardised transect walks for temporal trends in abundance) potentially requiring a greater investment in training of citizen scientists and data validation by experts. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

accessibility of such advanced data science techniques for entomological researchers is increasing, including through creative use of data science competitions to enhance inter-disciplinary collaboration (Humphries *et al.*, 2018).

Looking forward to the future of insect monitoring, we must take into account the root causes of our current data deficiency. Collection techniques have evolved through time and vary with location, but ready access to historical data is rare. Emerging technologies could facilitate the collection and availability of large quantities of data more cost-effectively, and at temporal and spatial resolutions that are currently not possible (Fig. 2b). Conservation genomics, for instance, takes an entirely different approach to assessing population size variation over time (Beichman *et al.*, 2018; Kent *et al.*, 2018; Noskova *et al.*, 2019). Bioacoustics is a rapidly maturing field of ecological data science, with extensive use in studies of marine mammals, birds, and some stridulating insects such as orthopterans. If we are less concerned with identification of species, but more with total abundance, then bioacoustics could also be applied to functionally relevant phenomena such as flower visitations based on insect buzzes (Jeliakov *et al.*, 2016). Another technology that is rapidly gaining traction in biological monitoring is the use of specialised entomological radar (Drake & Reynolds, 2012; Hu *et al.*, 2016; Wotton *et al.*, 2019) and more recently dopplerised weather radar networks, which may span continents (Hüppop *et al.*, 2019). Filtering the insect ‘noise’ from the meteorological signal in weather radar data can create a substantial, standardised

data set for insect monitoring through time (e.g. Stepanian *et al.*, 2020). Further advances in technologies such as light detection and ranging (LiDAR; Kirkeby *et al.*, 2016) and camera transects (Ruczyński *et al.*, 2020) offer the prospect of new tools in the future. In many cases, species-level identification can be a challenge with remote sensing methods and will require careful validation against conventional measures of insect population change (e.g. Wotton *et al.*, 2019; Stepanian *et al.*, 2020) until further tools are developed, but they show promise in helping to resolve some key issues in entomological data collection.

Finally, we encourage monitoring programmes to expand collaboration between citizen scientists and researchers (e.g. MacPhail *et al.*, 2019), in spite of some caution that has been raised about data quality, repeatability and taxonomic identification (Stribling *et al.*, 2008; Kremen *et al.*, 2011; Falk *et al.*, 2019). There may, however, be a need to revisit the relative costs and benefits of different citizen science approaches (including the opportunities and risks of integrating artificial intelligence; Wäldchen & Mäder, 2018; Ceccaroni *et al.*, 2019) in order to generate recommendations about which tools to adopt in insect population monitoring. The goals of citizen science programmes vary along a continuum from casual engagement to intensive standardised data collection (e.g. Fig. 2b), and effective citizen science programmes designed to monitor insect population trends should consider: (i) where along that continuum is optimal for the scale and quality of data that are required and (ii) how best to support the citizen scientists who take part in such activities



(training, rewards, etc) (van der Wal *et al.*, 2016). Note that these data and analytical considerations are inherently interlinked. Citizen scientists might help digitise museum collections to facilitate phenotypic and genetic analysis, as well as deploy bioacoustics sensors. Researchers might develop mathematical models that reveal previously unknown predictors, which can then be incorporated into future monitoring technologies. Radar technology might guide the design of citizen science monitoring schemes through stratified sampling of landscapes. Only through the full integration and cross-validation of these different data sources and approaches (Fig. 2a,b) will we be able to realise their full potential for monitoring insect population trends.

## Conclusions

We have made the case for a more critical approach to the study of ‘insect declines’ that avoids methodological errors to produce a robust analysis of population trends through time and the phenomena that drive them. We propose three key areas in which more focused attention is needed: on baselines, trends, and population-level understanding. The future is bright for insect monitoring, with new technologies coming online for the study of insect abundance. Nevertheless, the past remains dark due to the paucity of data. We suggest that overcoming the lack of historical context will require collaboration across ecological and statistical subdisciplines to share and cross-validate methods and datasets, in order to build a much more robust composite time series of current trends. These quantitative considerations are only part of the picture, of course, and may be a moot point if we do not reinforce the importance of insects and their conservation on the public and policy agenda (Saunders *et al.*, 2020b). The recent media attention creates an exceptional opportunity for improved public understanding and for broader funding of insect research. Just as for other components of biodiversity, raising the profile of insects and promoting a positive image may increase their perceived value to a wider sector of society and pay dividends for future conservation and restoration. A rich academic literature exists on the psychology and promotion of insects as food and feed (van Huis, 2017; Collins *et al.*, 2019), for instance, and this type of marketing approach applied to promoting the values of insects themselves could be a proactive way forward for insect conservation (Hart & Sumner, 2020). Once we reinforce this social licence to operate, we need to ensure that we have robust science to document ongoing trends and to support future action.

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## Conflict of Interest

The authors declare no conflict of interest.

## References

- Altermatt, F. & Ebert, D. (2016) Reduced flight-to-light behaviour of moth populations exposed to long-term urban light pollution. *Biology Letters*, **12**, 20160111. <<https://doi.org/10.1098/rsbl.2016.0111>> 14th December 2019.
- Andrewartha, H.G. (1961) *Introduction to the Study of Animal Populations*. Methuen & Co. Ltd, London, U.K.
- Baars, M.A. (1979) Catches in pitfall traps in relation to mean densities of carabid beetles. *Oecologia*, **41**, 25–46.
- Bahlai, C.A. & Zipkin, E.F. (2020) The dynamic shift detector: an algorithm to identify changes in parameter values governing populations. *PLoS Computational Biology*, **16**(1), e1007542. <<https://doi.org/10.1371/journal.pcbi.1007542>> 1st February 2020.
- Bartholomé, O. & Lavorel, S. (2019) Disentangling the diversity of definitions for the pollination ecosystem service and associated estimation methods. *Ecological Indicators*, **107**. <<https://doi.org/10.1016/j.ecolind.2019.105576>> 1st February 2020.
- Baum, K.A. & Wallen, K.E. (2011) Potential bias in pan trapping as a function of floral abundance. *Journal of the Kansas Entomological Society*, **84**, 155–159.
- Beichman, A.C., Huerta-Sanchez, E. & Lohmueller, K.E. (2018) Using genomic data to infer historic population dynamics of nonmodel organisms. *Annual Review of Ecology, Evolution, and Systematics*, **49**, 433–456.
- Bergmeir, C., Hyndman, R.J. & Koo, B. (2018) A note on the validity of cross-validation for evaluating autoregressive time series prediction. *Computational Statistics and Data Analysis*, **120**, 70–83.
- Bonebrake, T.C., Christensen, J., Boggs, C.L. & Ehrlich, P.R. (2010) Population decline assessment, historical baselines, and conservation. *Conservation Letters*, **3**, 371–378.
- Cardoso, P. & Leather, S.R. (2019) Predicting a global insect apocalypse. *Insect Conservation and Diversity*, **12**, 263–267.
- Cardoso, P., Branco, V.V., Chichorro, F., Fukushima, C.S. & Macías-Hernández, N. (2019) Can we really predict a catastrophic worldwide decline of entomofauna and its drivers? *Global Ecology and Conservation*, **20**, e00621. <<https://doi.org/10.1016/j.gecco.2019.e00621>> 29th November 2019.
- Cecaroni, L., Bibby, J., Roger, E., Flemons, P., Michael, K., Fagan, L. & Oliver, J.L. (2019) Opportunities and risks for citizen science in the age of artificial intelligence. *Citizen Science: Theory and Practice*, **4**(1), 29. <<https://doi.org/10.5334/cstp.241>> 26th January 2020.
- Chaput-Bardy, A., Grégoire, A., Bague, M., Pagano, A. & Secondi, J. (2010) Condition and phenotype-dependent dispersal in a damselfly, *Calopteryx splendens*. *PLoS One*, **5**(5), e10694. <<https://doi.org/10.1371/journal.pone.0010694>> 22nd January 2020.
- Cohen, J.M., Lajeunesse, M.J. & Rohr, J.R. (2018) A global synthesis of animal phenological responses to climate change. *Nature Climate Change*, **8**, 224–228.
- Collins, C.M., Vaskou, P. & Kountouris, Y. (2019) Insect food products in the western world: assessing the potential of a new “green” market. *Annals of the Entomological Society of America*, (Special Collection: Insects as Food and Feed), 1–11. <<https://doi.org/10.1093/aesa/saz015>> 4th February 2020.
- Corlett, R.T. (2016) Restoration, reintroduction, and rewilding in a changing world. *Trends in Ecology & Evolution*, **31**, 453–462.
- Dallas, T.A., Saastamoinen, M., Schulz, T. & Ovaskainen, O. (2020) The relative importance of local and regional processes to metapopulation

- dynamics. *Journal of Animal Ecology*. <<https://doi.org/10.1111/1365-2656.13141>> 4th February 2020.
- Dee, L.E., Cowles, J., Isbell, F., Pau, S., Gaines, S.D. & Reich, P.B. (2019) When do ecosystem services depend on rare species? *Trends in Ecology & Evolution*, **34**, 746–758.
- Denno, R.F. & Peterson, M.A. (1995) Density-dependent dispersal and its consequences for population dynamics. *Population Dynamics: New Approaches and Synthesis* (ed. by N. Cappuccino and P. W. Price), pp. p. 113–130. Academic Press, New York, NY.
- Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J. & Collen, B. (2014) Defaunation in the Anthropocene. *Science*, **345**, 401–406.
- Drake, V.A. & Reynolds, D.R. (2012) *Radar Entomology: Observing Insect Flight and Migration*. CABI.
- Enfjäll, K. & Leimar, O. (2005) Density-dependent dispersal in the Glanville fritillary, *Melitaea cinxia*. *Oikos*, **108**, 465–472.
- Falk, S., Foster, G., Comont, R., Conroy, J., Bostock, H., Salisbury, A., Kilbey, D., Bennett, J. & Smith, B. (2019) Evaluating the ability of citizen scientists to identify bumblebee (*Bombus*) species. *PLoS One*, **14**(6), e0218614. <<https://doi.org/10.1371/journal.pone.0218614>> 1st February 2020.
- Forister, M.L., Pelton, E.M. & Black, S.H. (2019) Declines in insect abundance and diversity: we know enough to act now. *Conservation Science and Practice*, **1**, e80. <<https://doi.org/10.1111/csp2.80>> 29th November 2019.
- Fournier, A.M.V., White, E.R. & Heard, S.B. (2019) Site-selection bias and apparent population declines in long-term studies. *Conservation Biology*, **33**, 1370–1379.
- Fox, R. (2013) The decline of moths in Great Britain: a review of possible causes. *Insect Conservation & Diversity*, **6**, 5–19.
- Fox, R., Harrower, C.A., Bell, J.R., Shortall, C.R., Middlebrook, I. & Wilson, R.J. (2018) Insect population trends and the IUCN Red List process. *Journal of Insect Conservation*, **23**, 269–278.
- Gallant, A.L., Euliss, N.H. & Browning, Z. (2014) Mapping large-area landscape suitability for honey bees to assess the influence of land-use change on sustainability of national pollination services. *PLoS One*, **9**(6), e99268. <<https://doi.org/10.1371/journal.pone.0099268>> 22nd January 2020.
- Gardiner, T. (2007) Short-term changes (2001–2005) in glow worm *Lampyrus noctiluca* L. (Coleoptera: Lampyridae) abundance in Essex. *British Journal of Entomology and Natural History*, **20**, 1–6.
- Gardiner, T. & Didham, R.K. (2020) Glowing, glowing, gone? Monitoring long term trends in glow-worm numbers in south-east England. *Insect Conservation & Diversity*, **13**.
- Gaston, K.J., Visser, M.E. & Holker, F. (2015) The biological impacts of artificial light at night. *Philosophical Transactions of the Royal Society Series B*, **370**, 20140133. <<https://doi.org/10.1098/rstb.2014.0133>> 2nd January 2020.
- Gezon, Z.J., Wyman, E.S., Ascher, J.S., Inouye, D.W. & Irwin, R.E. (2015) The effect of repeated, lethal sampling on wild bee abundance and diversity. *Methods in Ecology and Evolution*, **6**, 1044–1054.
- Habel, J.C., Trusch, R., Schmitt, T., Ochse, M. & Ulrich, W. (2019) Long-term large-scale decline in relative abundances of butterfly and burnet moth species across south-western Germany. *Scientific Reports*, **9**, 14921. <<https://doi.org/10.1038/s41598-019-51424-1>> 27th January 2020.
- Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hören, T., Goulson, D. & de Kroon, H. (2017) More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS One*, **12**, e0185809.
- Hallmann, C.A., Zeegers, T., van Klink, R., Vermeulen, R., van Wielink, P., Spijkers, H., van Deijk, J., van Steenis, W. & Jongejans, E. (2020) Declining abundance of beetles, moths and caddisflies in The Netherlands. *Insect Conservation and Diversity*, **13**, 127–139.
- Hanski, I. (1998) Metapopulation dynamics. *Nature*, **396**, 41–49.
- Hart, A.G. & Sumner, S. (2020) Marketing insects: can exploiting a commercial framework help promote undervalued insect species? *Insect Conservation and Diversity*, **13**, 214–218.
- Harvey, J.A., Heinen, R., Armbrrecht, I., Basset, Y., Baxter-Gilbert, J.H., Bezemer, T.M., Böhm, M., Bommarco, R., Borges, P.A.V., Cardoso, P., Clausnitzer, V., Cornelisse, T., Crone, E.E., Dicke, M., Dijkstra, K.D.B., Dyer, L., Ellers, J., Fartmann, T., Forister, M.L., Furlong, M.J., Garcia-Aguayo, A., Gerlach, J., Gols, R., Goulson, D., Habel, J.C., Haddad, N.M., Hallmann, C.A., Henriques, S., Herberstein, M.E., Hochkirch, A., Hughes, A.C., Jepsen, S., Jones, T.H., Kaydan, B.M., Kleijn, D., Klein, A.M., Latty, T., Leather, S.R., Lewis, S.M., Lister, B.C., Losey, J.E., Lowe, E.C., Macadam, C.R., Montoya-Lerma, J., Nagano, C.D., Ogan, S., Orr, M.C., Painting, C.J., Pham, T.H., Potts, S.G., Rauf, A., Roslin, T.L., Samways, M.J., Sanchez-Bayo, F., Sar, S.A., Schultz, C.B., Soares, A.O., Thancharoen, A., Tschamtker, T., Tylianakis, J.M., Umbers, K.D.L., Vet, L.E.M., Visser, M.E., Vujic, A., Wagner, D.L., WallisDeVries, M.F., Westphal, C., White, T.E., Wilkins, V.L., Williams, P.H., Wyckhuys, K.A.G., Zhu, Z.R. & de Kroon, H. (2020) International scientists formulate a roadmap for insect conservation and recovery. *Nature Ecology & Evolution*, **4**, 174–176. <<https://doi.org/10.1038/s41559-019-1079-8>> 6th February 2020.
- Hicks, B.J., Leather, S.R. & Watt, A.D. (2008) Changing dynamics of the pine beauty moth (*Panolis flammea*) in Britain: the loss of enemy free space? *Agricultural & Forest Entomology*, **10**, 263–271.
- Hill, J.K., Thomas, C.D., Fox, R., Telfer, M.G., Willis, S.G., Asher, J. & Huntley, B. (2012) Responses of butterflies to twentieth century climate warming: implications for future ranges. *Proceedings of the Royal Society of London, Series B*, **269**, 2163–2171.
- Hill, M.P., Gallardo, B. & Terblanche, J.S. (2017) A global assessment of climatic niche shifts and human influence in insect invasions. *Global Ecology and Biogeography*, **26**, 679–689.
- Holzschuh, A., Dormann, C.F., Tschamtker, T. & Steffan-Dewenter, I. (2011) Expansion of mass-flowering crops leads to transient pollinator dilution and reduced wild plant pollination. *Proceedings of the Royal Society of London, Series B*, **278**, 3444–3451.
- Howard, L.C., Wood, P.J., Greenwood, M.T. & Rendell, H.M. (2009) Reconstructing riverine paleo-flow regimes using subfossil insects (Coleoptera and Trichoptera): the application of the LIFE methodology to paleochannel sediments. *Journal of Paleolimnology*, **42**, 453–466.
- Hu, G., Lim, K.S., Horvitz, N., Clark, S.J., Reynolds, D.R., Sapir, N. & Chapman, J.W. (2016) Mass seasonal bioflows of high-flying insect migrants. *Science*, **354**, 1584–1587.
- Humphries, G.R.W., Che-Castaldo, C., Bull, P.J., Lipstein, G., Ravia, A., de Carrión, B., Bolton, T., Ganguly, A. & Lynch, H.J. (2018) Predicting the future is hard and other lessons from a population time series data science competition. *Ecological Informatics*, **48**, 1–11.
- Hüppop, O., Ciach, M., Diehl, R., Reynolds, D.R., Stepanian, P.M. & Menz, M.H.M. (2019) Perspectives and challenges for the use of radar in biological conservation. *Ecography*, **42**, 912–930.
- Isaac, N.J.B. & Pocock, M.J.O. (2015) Bias and information in biological records. *Biological Journal of the Linnean Society*, **115**, 522–531.
- Jeliazkov, A., Bas, Y., Kerbiriou, C., Julien, J.-F., Penone, C. & Le Viol, I. (2016) Large-scale semi-automated acoustic monitoring

- allows to detect temporal decline of bush-crickets. *Global Ecology and Conservation*, **6**, 208–218.
- Karlsson, D., Hartop, E., Forshage, M., Jaschhof, M. & Ronquist, F. (2020) The Swedish Malaise trap project: a 15 year retrospective on a countrywide insect inventory. *Biodiversity Data Journal*, **8**, e47255. <<https://doi.org/10.3897/BDJ.8.e47255>> 26th January 2020.
- Kent, C.F., Dey, A., Patel, H., Tsvetkov, N., Tiwari, T., MacPhail, V.J., Gobeil, Y., Harpur, B.A., Gurtowski, J., Schatz, M.C., Colla, S.R. & Zayed, A. (2018) Conservation genomics of the declining North American bumblebee *Bombus terricola* reveals inbreeding and selection on immune genes. *Frontiers in Genetics*, **9**, 316. <<https://doi.org/10.3389/fgene.2018.00316>> 22nd January 2020.
- Kirkeby, C., Wellenreuther, M. & Brydegaard, M. (2016) Observations of movement dynamics of flying insects using high resolution lidar. *Scientific Reports*, **6**, 29083. <<https://doi.org/10.1038/srep29083>> 26th January 2020.
- Komonen, A., Halme, P. & Kotiaho, J.S. (2019) Alarmist by bad design: strongly popularized unsubstantiated claims undermine credibility of conservation science. *Rethinking Ecology*, **4**, 17–19.
- Kremen, C., Ullman, K.S. & Thorp, R.W. (2011) Evaluating the quality of citizen-scientist data on pollinator communities. *Conservation Biology*, **25**, 607–617.
- Langor, D.W. (2019) The diversity of terrestrial arthropods in Canada. *The Biota of Canada – A Biodiversity Assessment. Part 1: The Terrestrial Arthropods* (ed. by D.W. Langor and C.S. Sheffield), Vol. **819**, pp. p. 9–40. ZooKeys. <<https://doi.org/10.3897/zookeys.819.31947>> 4th January 2020.
- Lebuhn, G., Droege, S., Connor, E.F., Gemmill-Herren, B., Potts, S.G., Minckley, R.L., Griswold, T., Jean, R., Kula, E., Roubik, D.W., Cane, J., Wright, K.W., Frankie, G. & Parker, F. (2013) Detecting insect pollinator declines on regional and global scales. *Conservation Biology*, **27**, 113–120.
- Leibrich, J. (2006) *Nesta and the Missing Zero*. Scholastic NZ Ltd, (ISBN: 1-86943-730-6).
- Lister, B.C. & Garcia, A. (2018) Climate-driven declines in arthropod abundance restructure a rainforest food web. *Proceedings of the National Academy of Sciences USA*, **115**, E10397–E10406.
- Lockwood, J.A. (2010) The fate of the Rocky Mountain locust, *Melanoplus spretus* Walsh: implications for conservation biology. *Terrestrial Arthropod Reviews*, **3**, 129–160.
- Macgregor, C.J., Williams, J.H., Bell, J.R. & Thomas, C.D. (2019) Moth biomass increases and decreases over 50 years in Britain. *Nature Ecology and Evolution*, **3**, 1645–1649.
- MacPhail, V.J., Richardson, L.L. & Colla, S.R. (2019) Incorporating citizen science, museum specimens, and field work into the assessment of extinction risk of the American Bumble bee (*Bombus pensylvanicus* De Geer 1773) in Canada. *Journal of Insect Conservation*, **23**, 597–611.
- Martin, B.T., Munch, S.B. & Hein, A.M. (2018) Reverse-engineering ecological theory from data. *Proceedings of the Royal Society of London, Series B*, **285**, 20180422. <<https://doi.org/10.1098/rspb.2018.0422>> 26th January 2020.
- McGeachie, W.J. (1989) The effects of moonlight illuminance, temperature and wind speed on light-trap catches of moths. *Bulletin of Entomological Research*, **79**, 185–192.
- Minnaar, C., Boyles, J.G., Minnaar, I.A., Sole, C.L. & McKechnie, A.E. (2015) Stacking the odds: light pollution may shift the balance in an ancient predator-prey arms race. *Journal of Applied Ecology*, **52**, 522–531.
- Møller, A.P. (2019) Parallel declines in abundance of insects and insectivorous birds in Denmark over 22 years. *Ecology and Evolution*, **9**, 6581–6587. <<https://doi.org/10.1002/ece3.5236>> 29th May 2019.
- Montgomery, G.A., Dunn, R.R., Fox, R., Jongejans, E., Leather, S.R., Saunders, M.E., Shortall, C.R., Tingley, M.W. & Wagner, D.L. (2020) Is the insect apocalypse upon us? How to find out. *Biological Conservation*.
- Mupepele, A.C., Bruelheide, H., Dauber, J., Krüß, A., Potthast, T., Wägele, W. & Klein, A.M. (2019) Insect decline and their drivers: unsupported conclusions in a poorly performed meta-analysis on trends—a critique of Sánchez-Bayo and Wyckhuys (2019). *Basic and Applied Ecology*, **37**, 20–23.
- Noskova, E., Ulyantsev, V., Koepfli, K.P., O'Brien, S.J. & Dobrynin, P. (2019) GADMA: genetic algorithm for inferring demographic history of multiple populations from allele frequency spectrum data. *BioRxiv*, 407734.
- Oliver, T.H., Powney, G.D., Baguette, M. & Schtickzelle, N. (2017) Synchrony in population counts predicts butterfly movement frequencies. *Ecological Entomology*, **42**, 375–378.
- Outhwaite, C.L., Chandler, R.E., Powney, G.D., Collen, B., Gregory, R. D. & Isaac, N.J.B. (2018) Prior specification in Bayesian occupancy modelling improves analysis of species occurrence data. *Ecological Indicators*, **93**, 333–343.
- Ovaskainen, O. & Saastamoinen, M. (2018) Frontiers in metapopulation biology: the legacy of Ilkka Hanski. *Annual Review of Ecology, Evolution and Systematics*, **49**, 231–252.
- Owens, A.C.S., Cochar, P., Durrant, J., Farnworth, B., Perkin, E.K. & Seymoure, B. (2020) Light pollution is a driver of insect declines. *Biological Conservation*, **241**, 108259. <<https://doi.org/10.1016/j.biocon.2019.108259>> 2nd January 2020.
- Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- Pilotto, F., Nilsson, C., Polvi, L.E. & McKie, B.G. (2018) First signs of macroinvertebrate recovery following enhanced restoration of boreal streams used for timber floating. *Ecological Applications*, **28**, 587–597.
- Pollard, E. (1991) Synchrony of population fluctuations - the dominant influence of widespread factors on local butterfly populations. *Oikos*, **60**, 7–10.
- Powney, G.D., Carvell, C., Edwards, M., Morris, R.K.A., Roy, H.E., Woodcock, B.A. & Isaac, N.J.B. (2019) Widespread losses of pollinating insects in Britain. *Nature Communications*, **10**, 1018. <<https://doi.org/10.1038/s41467-019-08974-9>> 29th November 2019.
- Ruczyński, I., Hałat, Z., Zegarek, M., Borowik, T. & Dechmann, D.K.N. (2020) Camera transects as a method to monitor high temporal and spatial ephemerality of flying nocturnal insects. *Methods in Ecology and Evolution*, **11**, 294–302. <<https://doi.org/10.1111/2041-210X.13339>> 26th January 2020.
- Rabl, D., Rabl, C. & Rabl, S. (2017) The Mediterranean distributed Cypress jewel beetle *Ovalisia festiva* (Linnaeus, 1767) has reached the east of Austria (Coleoptera: Buprestidae). *Entomologische Zeitschrift*, **127**, 109–111.
- Redfearn, A. & Pimm, S.L. (1988) Population variability and polyphagy in herbivorous insect communities. *Ecological Monographs*, **58**, 39–55.
- Régnière, J. & Nealis, V.G. (2019) Density dependence of egg recruitment and moth dispersal in spruce budworms. *Forests*, **10**, 706. <<https://doi.org/10.3390/f10080706>> 4th January 2020.
- Roquette, J.R. & Thompson, D.J. (2007) Patterns of movement and dispersal in an endangered damselfly and the consequences for its management. *Journal of Applied Ecology*, **44**, 692–701.
- Roubik, D.W. (2001) Ups and downs in pollinator populations: when is there a decline? *Conservation Ecology*, **5**(1), 2.
- Sánchez-Bayo, F. & Wyckhuys, K.A.G. (2019) Worldwide decline of the entomofauna: a review of its drivers. *Biological Conservation*, **232**, 8–27.

- Saunders, M.E., Janes, J.K. & O'Hanlon, J.C. (2020a) Moving on from the insect apocalypse narrative: engaging with evidence-based insect conservation. *BioScience*, **70**, 80–89.
- Saunders, M.E., Janes, J. & O'Hanlon, J. (2020b) Semantics of the insect decline narrative: recommendations for communicating insect conservation to peer and public audiences. *Insect Conservation and Diversity*, **13**, 211–213.
- Saunders, S.P., Farr, M.T., Wright, A.D., Bahlai, C.A., Ribeiro, J.W., Rossman, S., Sussman, A.L., Arnold, T.W. & Zipkin, E.F. (2019) Disentangling data discrepancies with integrated population models. *Ecology*, **100**(6), e02714. <<https://doi.org/10.1002/ecy.2714>> 22nd January 2020.
- Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarli, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J.C., Linsenmair, K.E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S. & Weisser, W.W. (2019) Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature*, **574**, 671–674.
- Simmons, B.I., Balmford, A., Bladon, A.J., Christie, A.P., De Palma, A., Dicks, L.V., Gallego-Zamorano, J., Johnston, A., Martin, P.A., Purvis, A., Rocha, R., Wauchope, H.S., Wordley, C.F.R., Worthington, T.A. & Finch, T. (2019) Worldwide insect declines: an important message, but interpret with caution. *Ecology and Evolution*, **9**, 3678–3680.
- Shortall, C.R., Moore, A., Smith, E., Hall, M.J., Woiwod, I.P. & Harrington, R. (2009) Long-term changes in the abundance of flying insects. *Insect Conservation and Diversity*, **2**, 251–260.
- Soga, M. & Gaston, K.J. (2018) Shifting baseline syndrome: causes, consequences, and implications. *Frontiers in Ecology and Environment*, **16**, 222–230.
- Speight, M.C.D. (1989) *Saproxyllic Invertebrates and Their Conservation*. Nature and Environment Series, Vol. **42**, pp. p. 1–79. Council of Europe, Strasbourg.
- Stepanian, P.M., Entekhin, S.A., Wainwright, C.E., Mirkovic, D., Tank, J.L. & Kelly, J.F. (2020) Declines in an abundant aquatic insect, the burrowing mayfly, across major North American waterways. *Proceedings of the National Academy of Sciences USA*, **201913598**. <<https://doi.org/10.1073/pnas.1913598117>> 26th January 2020.
- Stribling, J.B., Pavlik, K.L., Holdsworth, S.M. & Leppo, E.W. (2008) Data quality, performance, and uncertainty in taxonomic identification for biological assessments. *Journal of the North American Benthological Society*, **27**, 906–919.
- Sutcliffe, O.L., Thomas, C.D. & Moss, D. (1996) Spatial synchrony and asynchrony in butterfly population dynamics. *Journal of Animal Ecology*, **65**, 85–95.
- Thomas, C.D., Jones, T.H. & Hartley, S.E. (2019) “Insectageddon”: a call for more robust data and rigorous analyses. *Global Change Biology*, **25**, 1891–1892.
- Thomson, J.D. (2010) Flowering phenology, fruiting success, and progressive deterioration of pollination in an early-flowering geophyte. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, **365**, 3187–3199.
- Thomson, J.D. (2019) Progressive deterioration of pollination service detected in a 17-year study vanishes in a 26-year study. *New Phytologist*, **224**, 1151–1159.
- van der Wal, R., Sharma, N., Mellish, C., Robinson, A. & Siddharthan, A. (2016) The role of automated feedback in training and retaining biological recorders for citizen science. *Conservation Biology*, **30**, 550–561.
- van Huis, A. (2017) Edible insects: marketing the impossible? *Journal of Insects as Food and Feed*, **3**, 67–68. <<https://doi.org/10.3920/JIFF2017.x003>> 4th February 2020.
- Vogel, G. (2017) Where have all the insects gone? *Science*, **356**, 576–579.
- Wagner, D.L. (2019) Global insect decline: comments on Sánchez-Bayo and Wyckhuys (2019). *Biological Conservation*, **233**, 334–335.
- Wagner, D.L. (2020) Insect declines in the Anthropocene. *Annual Review of Entomology*, **65**, 457–480.
- Wäldchen, J. & Mäder, P. (2018) Machine learning for image based species identification. *Methods in Ecology and Evolution*, **9**, 2216–2225.
- Walther, G.-R., Roques, A., Hulme, P.E., Sykes, M.T., Pyšek, P., Kühn, I., Zobel, M., Bacher, S., Botta-Dukát, Z., Bugmann, H., Czúcz, B., Dauber, J., Hickler, T., Jarošík, V., Kenis, M., Klotz, S., Minchin, D., Moora, M., Nentwig, W., Ott, J., Panov, V.E., Reineking, B., Robinet, C., Semchenko, V., Solarz, W., Thuiller, W., Vilà, M., Vohland, K. & Settele, J. (2009) Alien species in a warmer world: risks and opportunities. *Trends in Ecology & Evolution*, **24**, 686–693.
- Ward, D.F., New, T.R. & Yen, A.L. (2001) Effects of pitfall trapping on the abundance, richness and composition of invertebrate catches. *Journal of Insect Conservation*, **5**, 47–53.
- Watt, A.D. & Hicks, B.J. (2000) A reappraisal of the population dynamics of the pine beauty moth, *Panolis flammea*, on lodgepole pine, *Pinus contorta*, in Scotland. *Population Ecology*, **42**, 225–230.
- Wepprich, T., Adrion, J.R., Ries, L., Wiedmann, J. & Haddad, N.M. (2019) Butterfly abundance declines over 20 years of systematic monitoring in Ohio, USA. *PLoS One*, **14**, e0216270.
- Westphal, C., Bommarco, C., Carré, G., Lamborn, E., Morison, N., Petanidou, T., Potts, S.G., Roberts, S.P.M., Szentgyörgyi, H., Tscheulin, T., Vaissière, B.E., Woyciechowski, M., Biesmeijer, J.C., Kunin, W.E., Settele, J. & Steffan-Dewenter, I. (2008) Measuring bee diversity in different European habitats and biogeographical regions. *Ecological Monographs*, **78**, 653–671.
- White, E.R. (2019) Minimum time required to detect population trends: the need for longterm monitoring programs. *BioScience*, **69**, 40–46.
- Wilf, P., Labandeira, C.C., Johnson, K.R., Coley, P.D. & Cutter, A.D. (2001) Insect herbivory, plant defense, and early Cenozoic climate change. *Proceedings of the National Academy of Sciences USA*, **98**, 6221–6226.
- Willig, M.R., Woolbright, L., Presley, S.J., Schowalter, T.D., Waide, R. B., Heartsill Scalley, T., Zimmerman, J.K., González, G. & Lugo, A.E. (2019) Populations are not declining and food webs are not collapsing at the Luquillo Experimental Forest. *Proceedings of the National Academy of Sciences USA*, **116**, 12143–12144.
- Winfrey, R., Fox, J.W., Williams, N.M., Reilly, J.R. & Cariveau, D.P. (2015) Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecology Letters*, **18**, 626–635.
- Wotton, K.R., Gao, B., Menz, M.H.M., Morris, R.K.A., Ball, S.G., Lim, K.-S., Reynolds, D.R., Hu, G. & Chapman, J.W. (2019) Mass seasonal migrations of hoverflies provide extensive pollination and crop protection services. *Current Biology*, **29**, 2167–2173.