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Methodological problems of the analyses of insect decline

Metodické problémy při analýzách úbytku hmyzu

Bachelor thesis

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Prohlášení

Prohlašuji, že jsem práci zpracoval samostatně a uvedl jsem všechny použité zdroje a literaturu. Tato práce nebyla využita jako závěrečná práce k získání jiného nebo obdobného druhu vysokoškolské kvalifikace.

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Abstract

In recent years, several studies reporting a severe decline of insect populations across several continents turned the spotlight on the problem of insect decline. However, the reported declining parameters may vary, and it is necessary to differentiate between declines in biomass, abundance, diversity, or geographical range reduction. This thesis aims to summarize how the conclusions about insect decline are shaped by the methods researchers use, especially by the variables they measure, emphasizing the potential methodological issues and limitations of the various facets of insect decline. Furthermore, we offer a brief digest of the most relevant potential biases and interpretative risks threatening population monitoring surveys. The review also provides concise insight into the state of knowledge on the matter of insect population trends.

Keywords: insects, insect decline, insect population trends, methodology, methodological issues

Abstrakt

V posledních letech se dostalo značné pozornosti studiím, které přinesly svědectví o významném úbytku hmyzu. Ve skutečnosti se však parametry, které tyto studie měřily a o jejichž poklesu informovaly, mnohdy liší. Je nutné rozlišovat závěry o snížení biomasy, abundance, diverzity anebo zmenšení geografického rozšíření. Tato práce shrnuje, jak jsou naše poznatky o úbytku hmyzu ovlivněny použitými metodami, především tím, jaké parametry jsou měřeny. Důraz je kladen na možné metodologické problémy a omezení, na něž naráží různé aspekty úbytku hmyzu. Dále práce nabízí stručný přehled těch nejzásadnějších systematických chyb a interpretačních překážek, které provázejí studium hmyzích populací. V neposlední řadě nabízíme i přehledové shrnutí současného stavu poznání hmyzích populačních trendů.

Klíčová slova: hmyz, úbytek hmyzu, populační trendy hmyzu, metodologie, metodologické problémy

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1 Introduction

In recent years, several studies reporting a disturbing decline of insect populations across several continents turned the spotlight on the problem of insect decline (Hallmann *et al.* 2017; Lister & Garcia 2018; Sánchez-Bayo & Wyckhuys 2019), and some even introduced the outlining crisis to the public as mass media were quick to adopt them (Vogel 2017; Jarvis 2018; The Economist 2019). In the US, the focus has been mainly on the already recognized “pollination crisis,” and the awareness slightly expanded on insect decline in general (Althaus *et al.* 2021). Outside of the US, the number of insect-focused reports increased (Althaus *et al.* 2021), informing the public about the issue, which to entomologists has been apparent for at least a decade (Conrad *et al.* 2004, 2006; Shortall *et al.* 2009).

However, the term “insect decline” is not self-explanatory. The declining parameters may vary, and it is necessary to differentiate between declines in biomass, abundance, diversity, or geographical range reduction. Studies have shown that the nature of the mutual relationships between the various aspects of decline is not trivial, and attention must be paid to precisely interpreting the available findings (e.g., Hallmann *et al.* 2020). That is why this work aims to epitomize how the conclusions about insect decline are shaped by the methods researchers use, especially by the variables they measure. The emphasis is on distinguishing the various facets of insect decline, as it is often thought of as a perspicuous expression. Nonetheless, it encompasses more *nonequivalent* phenomena, such as biomass decline, abundance decline, or diversity decline, which can be, at times, as far as mutually antithetical.

The structural footing of this work is drawn from the concept of *information content* (Munson *et al.* 2010). A study’s information content “is *its contribution* to the accurate and precise estimation of any underlying parameter of interest” (Isaac & Pocock 2015; emphasis added). In other words, the information content quantifies how much a study says about the actual value of a parameter that we strive to study, allowing for a simple comparison of datasets. The choice of the parameter of interest determines which aspect of insect decline will be investigated, and the value of information content decides how accurate estimation of the truth will be obtained.

The information content is relative to the selected studied parameter. That is why in the first chapter, we explore which variables were used in insect population research and what conclusions were reached, as the various metrics represent distinct facets of insect decline.

Naturally, the desire is to maximize the study’s information content, determined by its sub-elements, to get the most accurate and precise estimation of the truth. The information content’s key components are the temporal and spatial characteristics and the sampling method (Isaac & Pocock 2015), which are all discussed in the second chapter. We review related methodological and interpretational pitfalls that impact the veracity of our knowledge of insect population trends.

To sum up, first, we examine what exactly can be understood under “insect decline” while providing examples of already undertaken research and its output. Then we evaluate methodological problems and biases capable of distorting the results accenting such biases in available studies.

The focus of this work is not to disparage the few high-profile studies (Lister & Garcia 2018; Sánchez-Bayo & Wyckhuys 2019; Seibold *et al.* 2019) that recently reported alarming downward trends because they have already been extensively criticized across the spectrum of the scientific community (Komonen *et al.* 2019; Mupepele *et al.* 2019; Thomas *et al.* 2019; Wagner 2019; Willig *et al.* 2019; Daskalova *et al.* 2021). Several authors also offer insights on improving the methods used in the controversial studies rather than directly challenging conclusions of any specific paper (Simmons *et al.* 2019; Didham *et al.* 2020; Saunders *et al.* 2020a). This work aims to summarize what we have learned from the community reappraisal and what mistakes and shortcomings of our future endeavors we could eliminate.

Some authors have expressed concerns about the impact the alarming studies could have on the public perception of the scientific method and the veracity of information supplied by scientists because caution and a critical approach is necessary when examining the studies (Cardoso *et al.* 2019; Montgomery *et al.* 2020; Daskalova *et al.* 2021). In this context, even the semantics of the language used while presenting recent findings have been challenged and re-evaluated (Saunders *et al.* 2020b). If the uncertainty of our position is not clearly communicated, the emergence of information about the opposite trend, i.e., increase (Brooks *et al.* 2012; Fox *et al.* 2014), may jeopardize the public trust in the scientific method (Saunders *et al.* 2020b). As the time to critically analyze and possibly refine the methods and interpretation logic has come (Didham *et al.* 2020), we try to synthesize the numerous reasons why some of the already available works might not stand to close scrutiny, categorize some perilous practices and demonstrate the risks of using them. “Because of the enormous data gaps and potential biases, it is especially important to commit to elevated standards of study design, evidence, and communication” (Montgomery *et al.* 2020).

2 Aspects of decline

When considering population trends, a decline can be described as a reduction in several different parameters. None of the metrics alone provides evidence for a general insect decline; therefore, a combination of several metrics is required to conclude general decline (Habel *et al.* 2019). We present an analysis of the limitations that the various aspects of decline possess. Each metric is evaluated based on the evidence it delivers and the conclusions that it permits to draw. The limitations of each parameter are mentioned and demonstrated with examples. Contrast is drawn between the decline’s various facets to emphasize the need for precise interpretation of the results based on each of the variables.

2.1 Occupancy

Occupancy data are frequently used to assess data from museum collections, historical datasets, and opportunistic data from various volunteer surveys (e.g., DeWalt *et al.* 2005; Kuussaari *et al.* 2007). It is vital to consider the limitations of occupancy measures, as 35 out of 100 (35%) surveys reviewed were limited to

reporting occupancy. Out of the 39 papers that were based on empirical data (excluding duplicate datasets, anecdotal evidence, and one or two-year-long datasets) in the well-known review by Sánchez-Bayo and Wyckhuys (2019), 17 (43.6%) surveys reported occupancy (Saunders *et al.* 2020a). That illustrates how significant is the contribution of occupancy-based studies to the perceived insect decline.

Pairwise comparisons, which are usually statistically very weak, can prove effective when the focal variable is occupancy (Didham *et al.* 2020). However, the measuring of geographical ranges of species has several shortfalls. Generally, a comparison of grid cell occupancy over different time points (e.g., Desender & Turin 1989) may overlook correlations in the data, for instance, two species reacting together to one another or to a change of other influential covariates (Saunders *et al.* 2020a).

As an example of a study that successfully overcame these limitations, Paukkunen *et al.* (2018) studied the distribution and life cycle traits of Finland's cuckoo wasps over an extended period using data from collections and various ecological studies. They managed to show a correlation of trends in cuckoo wasps with their host species. Overall, they recorded that the eleven declining species were the small and rare ones usually nesting above ground.

Furthermore, data from databases or collections are usually under the influence of several biases (Fox *et al.* 2014). Species differ in their detectability which has to be accounted for, but even then, it is challenging to draw conclusions about anything else than intra-species patterns (MacKenzie *et al.* 2006). With a more extended period between the comparison time points, there is a chance that new sampling methods might improve the sampling efficiency of some species, introducing bias (Jeppsson *et al.* 2010). For example, improved light sources in light traps or attractant-based traps will significantly improve detectability. That is why Jeppsson *et al.* excluded records labeled as trapped from their study, as the progressive improvement of sampling methods would skew the records.

In contrast, Franzén and Johannesson (2007) adopted a different approach in their comparison of butterfly and moth populations at two time-points. While the baseline data was based on observation, in their new resurvey, they extensively used traps. They argue that since their study is limited to presence/absence data, elevated sampling effort is of benefit as it eliminates potential negative bias. Still, 27% of the species were not found in the present.

Furthermore, there is usually spatial and temporal variability in the recorder effort, and unique methods (Hill 2012) must be used to account for that (Fox *et al.* 2014; Habel *et al.* 2016). Museum collections are also subject to collection bias resulting in the overrepresentation of rare specimens (Guralnick & Van Cleve 2005; Grixti *et al.* 2009).

Van Strien *et al.* (2019) use quantitative analyses of the opportunistic citizen-science based data about butterflies. They argue that using correct methods, even this kind of citizen science data can be valuable, and the observation bias can be filtered out. They conclude that the collection bias against common species, which historically were not reported proportionally to rare species, cannot be accounted for, and therefore, the reported declines are overestimated. Other studies further explore the limits of the citizen-science data and its usability (van Strien *et al.* 2013; Isaac *et al.* 2014).

2.2 Biomass

Only a fraction of studies describing changes in insect populations measure biomass. From the 100 reviewed surveys explicitly focused on insect population trends, only nine (9%) reported biomass (Shortall *et al.* 2009; Hallmann *et al.* 2017, 2020, 2021; Lister & Garcia 2018; Homburg *et al.* 2019; Macgregor *et al.* 2019; Seibold *et al.* 2019; Vereecken *et al.* 2021). From the 166 datasets used in the meta-analysis by van Klink *et al.* (2020), which were, in general, initially not focused on reporting population trends and instead addressed more specific ecological questions, only 36 (21.7%) reported biomass.

The major limitation of aggregate biomass measurement is that detected changes can be driven by trends in a small number of the most common or the largest species. Such an increase or decline is strictly speaking a change in the populations of the trending species, not a change in insects in general.

2.2.1 Biomass in the Krefeld Entomological Society data

Hallman *et al.* described broad insect population declines in a 2017 study based on data collected by the Krefeld Entomological Society (Vogel 2017). The work reported a 75% decline in flying insect biomass over the last 25 years using a series of 96 unique time-place snapshots across 63 sites spread around Germany's protected areas (Hallmann *et al.* 2017). It is noteworthy that most of the locations were sampled only once or twice. The results were reported in the total biomass of all sampled flying insects; thus, the only information gained from this study is that biomass of flying insects in the studied parts of Germany was lower in 2014 than in 1989 by 75%.

The reported trend suggests that insects are declining, however, without further analysis, the biomass value does not describe the distribution of the losses. Total biomass declines might result from species richness decline, abundance decline, predominant loss of the heavier species, or any combination of these mechanisms (Hallmann *et al.* 2021). Aggregate biomass *alone* provides no other information than the decrease of insects available as food-source. Further analysis is required to obtain at least the total sample abundance, better still to gain information about species in the sample and their respective abundance (e.g., Homburg *et al.* 2019; Hallmann *et al.* 2020) to unveil how the losses were distributed among the species spectrum.

Authors of the 2017 study have recently published a follow-up analysis of the original data (Hallmann *et al.* 2021). In this new study, the authors aim to provide further insight into the relationships between different metrics. Two snapshots (1989, 2014) collected in the Wahnbachtal protected area were selected from the original data. Hallman *et al.* focused on hoverflies which were considered suitable bioindicators and potentially representative of other insect taxa. The authors identified all the hoverflies, established the number of hoverfly species, hoverfly abundance in the sample, and measured their body size. The total flying insect biomass, the abundance of hoverflies, and the number of hoverfly species were lower in 2014 than in 1989. Total hoverfly abundance was significantly correlated with total flying-insect biomass (Hallmann *et al.* 2021). Similarly, species richness was related to biomass, albeit non-linearly. The losses were also more significant in the formerly more abundant species, which was hypothesized as a cause of the severe biomass declines and which

may play a role in declines across trophic cascades affecting, for instance, insectivorous birds (Gardarsson 2008; Stanton *et al.* 2018; Bowler *et al.* 2019; Møller 2019).

The fact that the authors obtained data about the abundance of the species and their body length allowed them to conclude that it is unlikely that the observed declines in biomass were a result of lighter species replacing heavier ones, at least within the group of hoverflies, as no difference in the distribution of log body size was observed. This study shows the parallel of abundance and species richness decline *in hoverflies* with the decline of total flying insect biomass. The additional effort put into measuring the relative abundance and species richness allowed to draw the resulting comprehensive conclusions describing the distribution of biomass decline and the loss of abundance and diversity.

Other studies (Homburg *et al.* 2019; Macgregor *et al.* 2019; Hallmann *et al.* 2020) have tried to calculate biomass loss from the measured abundance of individuals and their average weight using the size-weight equations. However, Hallman *et al.* (2021) say that since these calculations are limited to one taxon, they cannot show the context of total biomass decline. The context indicates that the decline is probably widespread, at least as far as flying insects are concerned; however, the observed parallel between biomass and other parameters cannot be extrapolated to other insect taxa based on a study that uncovered trends of hoverflies which, as the authors inform, represented only 5% of the flying insect biomass.

2.2.2 Other examples of biomass focused studies

Others have tried to explore biomass trends combined with other metrics revealing the relationships between different aspects of insect decline.

Seibold *et al.* (2019) have observed arthropods on 150 grasslands and 140 forest sites around Germany across a gradient of land-use conditions. They have found that the slopes and directions of the reported population trends were dependent on the metric used. The losses in biomass and abundance in grasslands did not fully correspond with less severe species richness losses. More significantly, on forest sites, biomass and species richness dropped while abundance remained stable. The authors also report that in some of the studied locations, decline affected rare species more than common ones (Seibold *et al.* 2019; but see Daskalova *et al.* 2021).

Hallmann *et al.* (2020) analyzed long-term monitoring data (1997-2017) of moths and ground beetles in two locations in the Netherlands. The study showed that the decline in moth biomass was distributed among all the species not dependent on their weight. However, in ground beetles, smaller and less abundant species underwent a more severe decrease than common or large ones, which resulted in a smaller decline in the aggregate biomass of beetles compared to their abundance, exemplifying the potential disparity of different decline measures.

In contrast, Shortall *et al.* (2009) have observed a local decline in flying insect biomass driven by the largest common species. The study used data from four of the Rothamsted Insect Survey *suction traps* spread over Southern Britain, collecting specimens daily from 1973 to 2002. A significant decline was detected at only one of the four locations, corroborating considerable spatial variability in biomass. Moreover, specific taxa were

subject to site-specific changes across the sites, demonstrating the unpredictability of biomass change and possibly turnover dynamics. Such trends are consistent with other studies (Bell *et al.* 2015). Vereecken *et al.* (2021) hypothesize that the turnover dynamic may be responsible for the unpredictable relationship between biomass and species, functional and phylogenetic biodiversity metrics.

Similarly, Macgregor *et al.* (2019) provided insight into the scale of spatial and temporal variability of biomass in a study that draws its data from the Rothamsted Insect Survey *light trap* dataset consisting of data recorded across Britain between 1967 and 2017. Mean annual biomass from all sampling locations varied about twofold within each decade and sixfold over the entire study period. More significantly, at individual locations, annual biomass varied up to 50-fold across the study period and up to 28-fold within each decade (Macgregor *et al.* 2019).

The spatiotemporal variability has several consequences that place demands on studies aiming to report accurate biomass estimates. Short-term data will provide unreliable estimates of longer-term biomass change because biomass greatly varies across the sampling sites. Furthermore, “interval sampling (comparing first and last year of a sequence) incorrectly estimates the sign of regression-based 20-yr trends 24% of the time” (Macgregor *et al.* 2019). Those are critical findings, as almost all other existing biomass estimates lack continuous, systematically controlled monitoring or a sufficient number of survey sites.

The foregoing results imply that declines in biomass can indicate widespread insect loss, but there is also evidence for instances when the decline distribution is not entirely ubiquitous. Aggregate biomass is vulnerable to be driven by changes in large or common species and can becloud trends on species level. For instance, a minor decline in biomass may veil severe selective decrease in smaller species (Heleno *et al.* 2009; Homburg *et al.* 2019; Hallmann *et al.* 2020). In this case, measuring only biomass could result in a failure to pass necessary conservation decisions.

As already mentioned, there is a general assumption (Didham *et al.* 2020) that the significant aggregate declines in abundance and partially in biomass (Hallmann *et al.* 2017, 2020) must be driven by losses in abundant and common species rather than rare ones (Shortall *et al.* 2009). Moreover, common species might be more vulnerable than previously thought (Habel & Schmitt 2018), and they are essential in the provision of ecosystem services (Winfree *et al.* 2015). Biomass can be a better indicator of declines in common (Shortall *et al.* 2009; Hallmann *et al.* 2021) or large species (Montgomery *et al.* 2020), detection of which is the first step in their successful conservation.

2.2.3 The benefits of measuring biomass

Some advocate using biomass because it is easy to measure and does not require the taxonomical expertise needed to describe species-level trends. Therefore, it can serve as a simple quantifier that can help facilitate the establishment of standardized monitoring schemes (Cardoso & Leather 2019; Montgomery *et al.* 2020).

In this context, the relationship between biomass and other metrics was explored. Vereecken *et al.* (2021), who examined relationships of biomass, abundance, and various facets of diversity within wild bees,

conclude that while biomass was significantly and strongly correlated with abundance, it did not reliably reflect the diversity aspects of the insect community. The above-mentioned biomass studies suggest that the biomass-abundance relationship is generally less predictable than Vereecken *et al.* report.

Still, some authors postulate that biomass can be used to facilitate more straightforward quantification of abundance in the case of large sampling quantities when species identification and even counting are not feasible (Hallmann *et al.* 2017; Montgomery *et al.* 2020). On the other hand, others recognize the risks and limitations of using biomass (Shortall *et al.* 2009; Vereecken *et al.* 2021).

Biomass can be more appealing to the public, but correct and precise interpretation is required (Saunders *et al.* 2020a) as wrong conclusions are not unprecedented in public media. For instance, *The Guardian* informed about declines in insect abundance based on a study (Hallmann *et al.* 2017) reporting a decline in biomass (Carrington 2017).

2.3 Abundance

Abundance is the predominant focal variable of insect decline studies, as 51 of 100 (51%) reviewed studies investigated its changes. In their meta-analysis, Van Klink *et al.* (2020b) gathered 153 (out of 166, 92.2%) datasets recording abundance. Correspondingly, in another recent meta-analysis focused on long time-series surveys by Sánchez-Bayo and Wyckhuys (2021), 32 out of 51 (62.7%) datasets measured abundance.

The abundance of individuals in ecosystems plays a vital role in their functioning (Gaston & Fuller 2008; Kleijn *et al.* 2015; Winfree *et al.* 2015). This supports the importance of monitoring abundance levels. Since the world faces losses in both in the number of species and the abundance of animals, diversity monitoring is not the only priority (Dirzo *et al.* 2014).

Like other metrics, abundance has its limitations and shortfalls. Akin to biomass, trends in abundance can also be driven by changes in a few of the most common species reflecting a decline in a fraction of all species instead of widespread insect decline (Supp & Ernest 2014). Furthermore, abundance monitoring can be complicated by some intrinsic properties of insect communities, such as natural fluctuation.

2.3.1 Fluctuation in insect populations

In insects, the populations are known to be put through a significant inter-annual fluctuation, which can be driven by resource availability, environmental conditions, their life-cycle periodicity, or biotic interactions (Wallner 1987; Gaston & Lawton 1988; Marquis *et al.* 2019) even without anthropogenic disturbance (Ives *et al.* 2008).

By way of illustration, Marquis *et al.* (2019) monitored the abundance of leaf-chewing insects and analyzed their response to spring frosts and summer droughts. Over the 20 years, no overall decline in abundance was recorded. However, insects strongly responded to the weather events with recovery time ranging from 1 to 5 years resulting in significant weather-induced oscillation. Similarly, Ives *et al.* (2008) demonstrate that midges can undergo density fluctuation of six orders of magnitude in irregular cycles of 4-7 years.

This variability further complicates drawing conclusions about insect abundance as carefully chosen baseline data and consistent and meticulously organized sampling are required when monitoring long-term abundance trends (White 2019; Saunders *et al.* 2020a). This has extensive implications for insect conservation biology when monitoring trends (White 2019), determining the causes of detected changes (McCain *et al.* 2016), and classifying threatened species (Wilson *et al.* 2011)

As a result, spatially or temporally restricted estimates of abundance alone are not a robust basis for conservation decisions, as the abundance of species is just a fraction of the context. Abundant species tend to fluctuate more than rare ones (Gaston & Lawton 1988). Common species may also disproportionately contribute to the observed losses, resulting in their lower-than-expected persistence rate (Hallmann *et al.* 2021). Some local populations can survive for only a limited time, likely because of the instability of the populations themselves in connection to their dispersal rates (den Boer 1985).

In response, large monitoring programs with standardized sampling protocols, sufficient sampling effort, and geographical coverage can provide robust data for a comprehensive analysis of insect population trends. Exemplary monitoring networks have been operating in the UK for decades now. Rothamsted Insect Survey (RIS) encompasses daily sampling using suction traps and a network of light traps operated by educated volunteers all across the UK.

Recently, Bell *et al.* (2020) used yearly totals of data collected by both RIS suction and light traps for 47 years (1969-2016) to analyze the numbers of moths and aphids. The extent of the data allowed the authors to detect trends on two temporal scales. Even though the moth assemblages underwent a significant decline throughout the study (-31%), a clear decline-recovery dynamic was apparent within most of the decades. The aphid decline was statistically *non-significant*, and whereas the sensitivity analysis revealed that most common species drove the aphid abundance decline, in moths the losses were distributed evenly among the species. The RIS light trap data were used before, for instance, by Conrad *et al.* in 2006 and 2004.

2.3.2 General examples of abundance studies

One of the most comprehensive studies into general abundance decline is the meta-analysis by van Klink *et al.* (2020b) (see also Desquilbet *et al.* 2020; van Klink *et al.* 2020a, 2021). The authors gathered 166 datasets mainly focused on abundance, with a fraction of them reporting biomass or both metrics. The analysis concluded an average decline of 9% per decade in terrestrial insect abundance and an increase of 11% per decade in freshwater insect abundance.

Consequently, a critique was published, pointing out several alleged weaknesses of the study. Among the challenged attributes were the data inclusion criteria, specifically the fact that some included datasets came from manipulative experiments or recovery monitoring. Imperfections were further seen in the statistical analysis details (more details in Desquilbet *et al.* 2020). Van Klink and colleagues reflected some of the encountered errors and performed some additional tests to demonstrate that the revised results are still well within the original confidence intervals. Nevertheless, they rejected many of the claims made by Desquilbet *et al.*, emphasizing that the critique is putting unrealistic expectations on the available data. Van Klink *et al.*

acknowledge the geographical bias towards North America and Europe and remind that the utilized data do not permit generalizations of the detected average trends across space and taxonomical categories (van Klink *et al.* 2020a, 2021).

An interesting attempt to utilize historical collection data to compare relative abundance in North American bumblebees was made by Jacobson *et al.* (2018). They detected severe declines in several species, but most of the species had to be considered data deficient. Nevertheless, the authors claim that they successfully used collection data to quantify the relative abundance and not just occupancy.

Baranov *et al.* (2020) have observed short-term fluctuations of all measured metrics in freshwater insects thanks to continuous long-term monitoring. Furthermore, they report a drastic decline in abundance (81.6%), accompanied by increased species richness and evenness.

Guo *et al.* (2020) monitored migratory insects on an island in China for 15 years. They describe intra-annual fluctuation and overall dominance of agriculturally subsidized species (similarly Macgregor *et al.* 2019). The authors also demonstrate how the pests' natural enemies migrate alongside them and that abundance losses suffered in non-pest species can disturb natural pest control. Measuring relative abundance instead of biomass as opposed to Macgregor *et al.* (2019) helped the researchers learn more about the fate of individual species and overcome the danger of detecting decline driven by the larger species.

2.3.3 The ambiguity of abundance trends

We need data beyond abundance to distinguish widespread tendencies from asynchronous local population trends, and diversity reducing extirpations from species turnover.

First, monitoring on a larger spatial scale is required to detect more than just local population trends. Whether the extrapolation to meta-population (Hanski 1998) is ever even possible remains a question (McArdle & Gaston 1993). Brooks *et al.* (2012) studied carabid beetles in the UK and showed that overall abundance decline was masking difference between locations and habitats. Whereas some sites showed declines ranging between 28% and 52%, elsewhere, the authors recorded an increase of 48%.

Second, the trait analysis of functional diversity allows researchers to assess the health of the assemblage and differentiate between deteriorating extirpation and species turnover (Villéger *et al.* 2012). This allowed Dupont *et al.* (2011) to describe the selective decrease in long-tongued bumblebees while short-tongued species remained largely unaffected, which shed new light on the true nature of the overall abundance decline.

Aggregate abundance trends can potentially be driven by changes in the most abundant species, masking trends in abundance and diversity of rare species (Supp & Ernest 2014). Sensitivity analysis can detect whether the trends are dependent on a limited number of strong species-level trends (Bell *et al.* 2020). That is why finer taxonomical resolution provides greatly improved information content.

2.4 Diversity

2.4.1 Species richness

Measuring species richness is very common when possible. Half of the reviewed studies (50) estimated species richness, whether based on field measurements or from the data in historical databases and museum collections. No relationship can be reliably pronounced between biomass or abundance and diversity metrics. Measuring diversity provides another piece of context into the mosaic of different aspects of insect decline.

For example, Homburg *et al.* (2019) studied carabid beetles in Germany, and whereas they did not observe any change in abundance, species richness and phylogenetic diversity declined. Were the study limited to mere abundance measures, these losses would remain unreported. Total abundance alone cannot reveal impoverishment in species richness.

In a different study, moth abundance decreased, but species richness increased. The authors hypothesized that even though overall abundance trends were downward, climate change caused species areas to shift and increased local species richness through more overlaps (Antão *et al.* 2020). A similar phenomenon was observed by Baranov and colleagues (2020) in freshwater insects on a site in Germany.

Species richness also proved to be practical when using museum or historical data as a baseline (e.g., Biesmeijer *et al.* 2006; Colla & Packer 2008; Grixti *et al.* 2009; Bommarco *et al.* 2012; Carvalheiro *et al.* 2013; Figueroa & Bergey 2015). It can be used with often brief data from historical databases and museum collections when studying changes in occupancy. This allows for a better characterization of the historical local population, which can potentially be used as baseline data for a long-term comparison (Guralnick & Van Cleve 2005).

2.4.2 Evenness

Each diversity measure must be carefully interpreted in its context. An increase in diversity is not always evidence of improvement. Evenness was reported by 14% of the reviewed studies providing vital context; it is not, however, suitable for quantifying decline.

For example, a decrease in the most abundant species will result in increased evenness and, in that regard, increased diversity (e.g., Crossley *et al.* 2020; Hallmann *et al.* 2021). In this context, the two aspects of decline have entirely opposite directions. The increase in evenness may have negative consequences for the ecosystem functions because the dominant species may play an essential role in the ecosystem (Winfree *et al.* 2009; Gaston 2010; Kleijn *et al.* 2015).

On the other hand, decrease in evenness (e.g., Bommarco *et al.* 2012; Powney *et al.* 2019) may be caused by a disproportionate decline in less abundant species, which can also negatively impact the ecosystem services and diversity of interacting organisms (e.g., pollinators and plants) (Fründ *et al.* 2010).

This is an example of the two aspects of insect decline, diversity, and biomass/abundance, changing in precisely opposite directions. Reporting limited to one of the metrics will be potentially misleading. Nevertheless, evenness changes can indeed indicate a recovery of an ecosystem and thus pose a good sign (e.g., Weller & Bossart 2017).

2.4.3 Phylogenetic diversity

There is some evidence that phylogenetic diversity might impact the resilience and stability of communities (Cadotte *et al.* 2012). That would substantiate its use as a focal variable when studying insect decline. Most notably, with the broader availability of phylogenetic methods, it is being considered as a proxy for other types of diversity, mainly functional diversity (Srivastava *et al.* 2012; Winter *et al.* 2013). It may further help to understand interactions between organisms and to uncover extinction cascades (Srivastava *et al.* 2012). Some authors point out that apart from quantifying the rarity and richness aspects and possibly being a proxy for functional diversity and evolutionary potential, there is little justification for using phylogenetic diversity in conservation research (Winter *et al.* 2013).

The relation between phylogenetic diversity and functional diversity, however, remains uncertain, with evidence speaking for both sides (Fritz & Purvis 2010; Mouquet *et al.* 2012). In insects, studies recommending using phylogenetic diversity measures at least as complementary variables to other biodiversity metrics appeared (Cardoso *et al.* 2016; Vereecken *et al.* 2021). For the time being, the relationship between phylogenetic diversity and Linnean systematics has been explored, not yet considering the relation to functional diversity (Vereecken *et al.* 2021). So far, phylogenetic diversity remains a marginal focal variable (Arnan *et al.* 2018; Homburg *et al.* 2019; Vereecken *et al.* 2021).

2.4.4 Functional diversity

Quantification of functional diversity and its changes can help determine the functional contribution of certain species like Jain *et al.* (2014) have done with rare species. Analysis of the functional diversity changes can also help predict the impact of population trends on the ecosystem.

For example, Biesmeijer *et al.* (2006) studied plant-pollinator interactions in the UK and the Netherlands using database records. The study showed that losses in pollinator populations had little impact on plant diversity when the functional characteristics of pollinating insects remained similar. Therefore, functional diversity can also help distinguish species turnover from community changes that impact the ecosystem's functioning.

2.5 Synthesis

While each metric can record a decline that can be conveyed as “insect decline,” in actuality, it presents just a fraction of the context. Currently, no consensus has been reached as to what “insect decline” means. Therefore, to conclude general insect decline, comprehensive analyses about species assemblages, abundances, and biomass, relating species traits to the prevailing environmental conditions, are needed (Habel *et al.* 2019). The examples of studies and their analysis led us to conclude that no single metric measuring is sufficient. The most valuable results are delivered by the studies that combine several mentioned metrics (e.g., Honek *et al.* 2014; Homburg *et al.* 2019; Høye *et al.* 2021; Vereecken *et al.* 2021).

3 Dimensions of the study

The critical components of the study's information content are the temporal and spatial characteristics and the sampling method (Isaac & Pocock 2015). The maximization of the information amount provided by the study happens through the adjustment of these three parameters. Based on the study's character, different aspects will be crucial. When measuring species richness, spatial features will be paramount. Alternatively, for detecting population trends, the temporal features will decide (Isaac & Pocock 2015).

However, the underlying assumption here is that the data we get by measuring are true or good enough approximation to the truth (Isaac & Pocock 2015). It is not always the case, as the biological data are often inherently biased (e.g., recognized in Prendergast *et al.* 1993). Therefore, preventing bias is vital for any combination of spatial, temporal, and sampling characteristics. From the various types of bias (Isaac & Pocock 2015), the most relevant or specific for insects will be discussed.

It should be noted that while most methods are innately biased, not all biases can be removed. Some types of bias must be standardized and quantified to be accounted for during the analysis (Montgomery *et al.* 2021). Eliminating bias is a vital step toward *interoperability* of the obtained data and complementarity of the various studies. While we do not provide a comprehensive guide for choosing the location or baseline data for a survey, we mention several logical and practical principles that should be considered when designing a study for monitoring insect populations in order to maximize the information content of the study.

3.1 Spatial dimension

The spatial characteristics that determine the information content of the study are simply the geographical range of the records (Isaac & Pocock 2015). From the global need perspective, attention should be given to the choice of the study location as current literature on insect population trends is subject to strong geographical bias, with North America and Europe handsomely outnumbering the rest of the world in insect population surveys (Cardoso & Leather 2019). The Afrotropic realm remains the most understudied, with other tropic regions closely behind (Saunders *et al.* 2020a). There is a strong suspicion that the results from regions most affected by human presence will poorly reflect situations across some less affected areas (Gonzalez *et al.* 2016). With few studies from the neotropics, it remains to be seen (e.g., Schowalter *et al.* 2021).

3.1.1 Geographic scope

Habel *et al.* (2019) argue that most of the available surveys have a restricted geographical scope (e.g., Habel *et al.* 2016). Therefore, our current knowledge consists mainly of local tendencies lacking information about large-scale effects that may be more relevant for the conservation of biodiversity as a whole. Others demonstrated that the spatial variability and potential asynchrony of local fluctuation of insect population could mean that large-scale generalizations may become misleading and inevitably becloud trends on finer spatial resolution.

For example, two studies examining carabid beetles, one in Britain and the other in Germany, recorded the opposite direction of the reported trends. Homburg *et al.* (2019) reported a decline of small species but no

change in large ones. On the other hand, Brooks *et al.* (2012) reported a decrease in large species. Brooks *et al.* also found spatial variability in the direction of the trends. Similarly, a particular species of bumblebee in North America recorded a decline in Ontario (Colla & Packer 2008), was data deficient in New Hampshire (Jacobson *et al.* 2018), and remains stable in Oklahoma (Figueroa & Bergey 2015).

3.1.2 Number of replications

Montgomery *et al.* (2021) reason for maximizing the number of spatial replications as it provides flexibility for the subsequent analysis. With the risk of pseudoreplications (Hurlbert 1984; e.g., Daskalova *et al.* 2021) in mind, it might be concluded that the more spatial replications, the better. With uniform spatial coverage over large enough territory, studies can provide enough data for two levels of analysis, local and regional. In practice, the spatial coverage and number of replications are limited by time, money, and other resources. The most effective way is to join an existing program which is already operating with standardized methods. Additional studies will broaden its reach, and data interoperability will be secured (Montgomery *et al.* 2021). Another thing to consider when deciding for the spatial situation of a study is that planning the survey across a gradient of light pollution, agricultural intensification, pesticide use, plant invasion, urban heat island, human density, or other disturbance could provide an understanding of what factors are contributing to insect declines and the intensity of such effects (Montgomery *et al.* 2020).

When selecting specific sites for a survey, several potential biases must be considered and preferably prevented, as described below.

3.1.3 Site selection bias

When designing an experiment monitoring virtually any animal population, there is a risk of site selection bias. The principle is that when study sites are selected, one might choose them in dependence on or in correlation with the abundance of the monitored species or taxon. This phenomenon is a manifestation of regression to the mean. For logistical and other reasons, sites where the species or taxon of interest are relatively abundant might be favored. Such bias will result in inflated or misleading results because the baseline for the experiment is more probably near the population peak rather than the trough (Forister *et al.* 2016).

A similar effect was noted by Pechmann, who realized such bias while studying amphibian populations that, similarly to insects, exhibit significant interannual fluctuations (Pechmann *et al.* 1991). The bias was also later described by Palmer (Palmer 1993). Some authors have tried to evaluate just how imminent the threat of the bias is and what consequences it might have (Fournier *et al.* 2019; Mentges *et al.* 2021). Simulations using both generated and real-life data showed that incidental site selection bias significantly impacted the detected trends. It was observed even to revert the direction of the occurring trend.

More importantly, however, the authors hypothesize a possible detection mechanism for such bias and a possible solution for data encumbered by it. Both the symptoms and the solutions to the site selection bias are

analogous to those of the wrong choice of baseline data discussed later. Left-censoring data¹ by some (usually artificially determined) amount can partially eliminate the effects of the bias (Fournier *et al.* 2019).

The authors also offer recommendations for future studies. For the sake of transparency, studies should explicitly mention the site selection methods (Coppolillo *et al.* 2004; Fournier *et al.* 2019). Furthermore, researchers should employ random sampling of the electable habitat or at least carefully consider the spatial variation of population trends (Yoccoz *et al.* 2001; Fournier *et al.* 2019; Weiser *et al.* 2019). The risk of non-random selection can also be weighted out by pairing manually selected sites with randomly selected counterparts (Fournier *et al.* 2019).

There is also a reverse selection bias occurring when monitoring rare species. A study initialized on locations with the abundance below average will bear artifacts of the same regression to the mean principle, and an inflated recovery may be detected (Palmer 1993; Fournier *et al.* 2019; Mentges *et al.* 2021).

The bias is relevant for both abundance and diversity monitoring (Mentges *et al.* 2021). A literature review also showed that the original articles mentioning the possible site selection bias were cited only three times in direct connection with the argument of the bias, which indicates this risk of non-random site selection might be underestimated (Fournier *et al.* 2019). The risk of site selection bias when studying insects is supported by their significant interannual variability (Pechmann *et al.* 1991; Gibbs *et al.* 1998). It is encouraging, however, that applying left-censoring on the data as a possible solution works better when monitoring species with a shorter generation time (Fournier *et al.* 2019). Therefore, in insects, the effect of censoring might be enough to filter out the initial bias.

3.1.4 The missing zero effect

With a close connection to the site selection bias, the so-called missing zero effect (Didham *et al.* 2020) refers to the consequences of underrepresenting potentially occupiable, however, unoccupied sites in the estimate of the average local abundance at the study baseline. Not including enough unoccupied sites with suitable habitats and accessible by dispersal will result in the inflation of the baseline abundance value (Hanski 1998; Ovaskainen & Saastamoinen 2018).

Consequently, previously occupied sites with a relatively high abundance of focal species may record a decline. However, the study will not reflect the potential increase in abundance on the previously unoccupied sites (Didham *et al.* 2020), which were not included in the study due to the site selection bias (Fournier *et al.* 2019). This will be especially significant when populations are influenced by density-dependent factors and asynchronous fluctuations among subpopulations (Pollard 1991; Sutcliffe *et al.* 1996). Interpolating the data obtained in surveys affected by the missing zero effect will be inaccurate because meta-populations might be only marginally influenced by the asynchronous fluctuations of their subpopulations (Pollard 1991). That is not to say that synchronous fluctuation caused by regional stochasticity cannot occur. For example, spatially correlated weather conditions might result in synchronous tendencies (Hanski 1998).

¹ Censoring in this context means intentional removal of data entries below a certain value (left-censoring) or above a certain value (right-censoring).

3.1.5 Consequences of the Wallacean shortfall

The spatial considerations of the experimental design are further complicated by the so-called Wallacean shortfall (Lomolino 2004). Our knowledge of insects is so limited that we do not know the geographical distribution of most species. Consequently, the distribution data are not complete and are mainly available on sites that are of special interest or are preferred by individual researchers. Such data are inherently biased (Hortal *et al.* 2007). This can result in biased site selection or cause the missing zero effect.

3.2 Temporal dimension

The relevant temporal characteristics of any study are the timespan of the records, the rate at which records are produced each year, and phenological scope (e.g., Were records produced during the whole year? How consistent were the records between years?) (Bishop *et al.* 2013; Isaac & Pocock 2015). Researchers are often limited by time, money, and workforce; hence care must be given to establishing an appropriate ratio between the amount of spatial and temporal replications (Rhodes & Jonzén 2011). Therefore, this section will review sundry issues affecting the temporal side of the experiment design.

Both the inter-annual and intra-annual replications improve the information content of the study and allow flexibility in the analysis. However, until now, many researchers had to overcome a general lack of historical baseline data (Cardoso *et al.* 2011; Cardoso & Leather 2019; Eisenhauer *et al.* 2019) either by retrospectively examining museum collections and historical datasets or even by inventing analytical methods to unlock the potential of opportunistic citizen-science data. That means that many long-term studies lacked the opportunity to consider the particularities of experimental design, obtain their own standardized baseline data or optimize the number of replications. To answer the many questions about insects and their populations, researchers were forced to work with the already available data. As a result, many papers are either limited to occupancy measures, deficient in the standardization of methods (e.g., Colla & Packer 2008), suffering from various biases (Guralnick & Van Cleve 2005; Isaac *et al.* 2014; Isaac & Pocock 2015) or lack reliable quantification of their uncertainty.

Nevertheless, some works fall short of expectations even if given a chance to consider the various facets of methodology. Whether it is due to resource limitations, by mistake, or just because the focus of the study was initially different than to fall in place with other works about general population trends of insects.

3.2.1 Baseline data

The precondition for any comparison of historical values with their current state is finding a quantitative estimate of a historical value of the focal variable, which will serve as a baseline for the study. To provide at least some insight into how insect populations changed over the last century and overcome the lack of baseline data, attempts have been made to utilize historical records and compare them with appropriate present data (e.g., van Strien *et al.* 2013). The researchers, therefore, cannot optimize the temporal setting of the study as the baseline is already set.

Historical datasets suffer from several shortcomings. The methods used to collect the data may be unknown or just vaguely described (e.g., Kosior *et al.* 2007). The same goes for the exact location of the survey and the sampling effort (e.g., Burkle *et al.* 2013). The data were usually collected for a different purpose than a long-term comparison and using it can result in numerous biases (Guralnick & Van Cleve 2005).

The collection time is often arbitrarily chosen without considering that the results might be used as baseline data for comparison in the future. Therefore, nothing is known about the trends that precede the captured moment (Didham *et al.* 2020). For example, a study reporting decline in moth population in the period from the 1980s to the present, supplied by the data from the preceding period (1967-1982), shows that the moth populations were originally even lower than today, peaked in the 1980 and kept declining ever since (Macgregor *et al.* 2019). Without the data from before 1982, the persistent decline would be reported without the previous context. Also, Seibold *et al.* (2019) acknowledge that the decline they report is driven partly by the first year of the study being a peak year with rich insect abundance.

This serves as an example of the shifting baseline syndrome; the perception of the current state is dependent on the level of our knowledge of historical conditions. This phenomenon stands as a challenge in tackling a number of environmental issues (Pauly 1995; Soga & Gaston 2018). Montgomery *et al.* (2020) also argue that shifting baseline syndrome may pose a problem as younger people have not witnessed the loss of insects with their own eyes and lack this albeit anecdotal evidence.

Furthermore, accurate historical baseline data are even more scarce. Most of the census studies begin only after the perceived beginning of the decline, intending to examine the presumed change (Bonebrake *et al.* 2010). Therefore the baselines might generally underestimate the actual original states of the populations, and recent studies (e.g., Powney *et al.* 2019) might document just a portion of the decline that has been occurring for a longer period (e.g., Carvalheiro *et al.* 2013). This will also result in the post-dating of the drivers of the change because the research starts only after the drivers have been around for some time (Montgomery *et al.* 2020).

The risk when establishing a historical baseline using data collected to answer an unrelated ecological question is that such data might not meet the statistical requirements for long-term population study (Didham *et al.* 2020) and might result in site selection bias (Fournier *et al.* 2019). It is perilous to use historical data with no specific methodology as proxies for the sought historical baseline (Bonebrake *et al.* 2010).

Population studies might therefore bear artifacts of either of these biases. The false baseline effect appears when the historical abundance is incorrectly estimated. The shifting baseline effect occurs when the historical abundance is estimated accurately, but there is still no evidence about the trends that led to that point in time (Didham *et al.* 2020).

3.2.2 Endline data

Similarly, as with the selection of a historical baseline, the contemporary time-point intended for comparison with the historical data has to be considered carefully (Didham *et al.* 2020).

An example of how distorted the results can be when the contemporary snapshot is not selected or interpreted correctly is Lister's and Garcia's (2018) study comparing two snapshots of insect populations in an experimental forest in Puerto Rico (Lister & Garcia 2018). The Luquillo experimental rainforest has a strong disturbance-driven dynamic caused by periodical decimation by hurricanes. As an independent study reported, the authors of the now refuted study chose a contemporary snapshot that recorded the rainforest in a succession stage following the last hurricane. The state of the community was not comparable to the original historical baseline. As opposed to the original paper, the new analysis recorded the data annually, which allowed the authors to describe the population trends caused by the natural succession driven by the occasional hurricanes (Schowalter *et al.* 2021). Lister and Garcia reported a decimating decline in populations of both insects and entomophages, which was interpreted as a collapse of established food webs caused by climate change (Lister & Garcia 2018). However, the independent study, thanks to the consistent annual sampling, demonstrated how the populations react to the succession restarted by the hurricanes and did not record any overall decline (Schowalter *et al.* 2021).

3.2.3 Duration of the study

There is a growing pile of evidence for the importance of long-term studies, with insect populations usually representing a worst-case scenario because of their innate ecological traits, such as population fluctuation. Insect populations fluctuate both inter-annually and within the same year. The oscillation can be driven by a variety of factors such as natural predators (Turchin *et al.* 1999), weather (Wolda 1992; Nelson *et al.* 2013; Ewald *et al.* 2015; Marquis *et al.* 2019), and peculiarities of their life cycles (Hanski 1990) sometimes resulting in complex dynamics with a period of several years (Ives *et al.* 2008).

This makes short-term surveys or studies comprising just a few "snapshots" very problematic (Habel *et al.* 2019; Didham *et al.* 2020) as the context of what happened between the snapshots is missing. The length of a time series needed to overcome the short-term fluctuation is directly proportional to both the period and amplitude of short-term variation (Woiwod & Harrington 1994, as cited in Conrad *et al.* 2007). Short-term studies tend to report more dramatic trends and are susceptible to various biases (White 2019; Daskalova *et al.* 2021)

Long-term studies are not only more valued in the scientific community, but compared to shorter studies, also disproportionately impact policymakers. On the other hand, short-term studies are more likely to receive funding (Hughes *et al.* 2017). Longer studies have a better chance of revealing non-linear trends in population abundance, and as the statistical approaches detecting non-linear trends are gaining traction (Macgregor *et al.* 2019; Høye *et al.* 2021), so rises the importance of long enough surveys (Giron-Nava *et al.* 2017). Gonzalez *et al.* (2016) point out how meta-analyses using short-term studies are systematically biased and can report false results.

Pairwise point estimates of local population change are a series of just two points and should be treated as such. They can prove effective in comparing differences in occupancy over time. However, they have little

statistical power when the compared variable is abundance unless the number of spatial replications is very high (Didham *et al.* 2020).

The core of the hereby presented problem is the more general concept of statistical power. This concept is by far not a new idea (Thomas 1996; Thomas & Krebs 1997; Gibbs *et al.* 1998), but in the past, some authors considered it to be perhaps slightly underappreciated in ecological research (Legg & Nagy 2006; White 2019).

For instance, in a study focused on the detection of trends in bee populations, Lebuhn *et al.* (2013) used power analysis to estimate that to gain enough statistical power to detect 2-5% annual decline in species richness and total abundance, 200-250 sampling locations sampled twice over five years are needed. Detecting smaller annual declines of 1% would see the number of sampling locations raised to >300.

In a different case, the authors estimated the coefficients of variation of abundance of different taxa, which they consequently used in a power analysis to determine the number of sampled plots or subpopulations needed to detect the annual decline of different intensities in a 10-year long period. To detect a decline of 10% over ten years, 120 locations were needed for moths, 190 for butterflies, and 260 for drosophilid flies with plots or subpopulations sampled five times a year. Dialing the sampling frequency down to once a year will raise the number of required locations to more than 500 for all the arthropod taxa (Gibbs *et al.* 1998). In contrast to the simulations run by Lebuhn *et al.* (2013), Gibbs *et al.* (1998) considered $\alpha = 0.1$ instead of $\alpha = 0.05$.

Finally, White (2019) used a similar approach but focused on the number of years or time points needed to estimate the trends in abundance via both simulation and empirical tests using retrospective power analysis (Thomas 1997). White demonstrates that, on average, at least 15 time points are required to detect a significant trend. The power of an analysis is increased when the trend or the autocorrelation of the population abundance is unusually strong. White further concludes that power analysis should be used more often.

To examine whether some snapshots play a disproportional role in our results (e.g., Seibold *et al.* 2019), it is possible to employ right-censoring of the data, a procedure similar to the suppression of an initial site selection bias (left-censoring). It is possible to remove a certain portion of the data chronologically preceding our contemporary time-point, e.g., remove data from the last two years (for more details, see Fournier *et al.* 2019; Didham *et al.* 2020).

White's (2019) findings have also stirred some debate over the pertinence of the IUCN classification criteria for insects. The 10-year evaluation period for endangered species may not be enough to detect a decline in a data stream as hectic as insect populations can be (van Swaay *et al.* 2011; Connors *et al.* 2014).

3.2.4 Snapshot data

Even though longitudinal studies (e.g., Conrad *et al.* 2004, 2006; Wepprich *et al.* 2019; Bell *et al.* 2020) provide more statistical power (White 2019), studies limited to a small number of snapshots can prove useful when continuous data is not available. The pairwise comparisons are employed when adopting creative approaches to unlocking unorthodox data for analysis, such as museum collections (Guralnick & Van Cleve 2005), notes from field trips (Breed *et al.* 2013), or opportunistic citizen-science data (van Strien *et al.* 2013).

However, such data must be used with caution and only if researchers control the variation in sampling effort and inconsistency of methodology, either through data filtering or direct statistical modeling. The survey must also be replicated on the same geographic scale as the baseline data (Tingley 2017; Montgomery *et al.* 2020).

The option of using historical data did not go unnoticed as, for instance, 56% of the studies in Sánchez-Bayo's and Wyckhuys's 2019 review used museum data of distribution as baseline data for their analysis. However, museum data especially tend to suffer from varying geographical coverage, sampling effort, and collector bias, i.e., when a disproportionate amount of rare species is included in the collections while underrepresenting common species (Guralnick & Van Cleve 2005; Grixti *et al.* 2009).

3.2.5 Temporal pseudoreplications

Daskalova *et al.* (2021), in their recent study, point out that many ecological studies (Seibold *et al.* 2019) do not include in their mixed effect models the random year effect. Inter-annual pseudoreplications are under the joint influence of many environmental conditions, and the data are not mutually independent. The year effects and their intensity were further examined by Werner *et al.* (2020). However, we already know that year-specific weather events may have a strong, temporally limited effect on insect populations (Ewald *et al.* 2015; Marquis *et al.* 2019).

When analyzing population tendencies, temporally or spatially fluctuating factors that affect the number of sampled individuals, such as the year effect, should be incorporated as covariables or otherwise considered. The detected trends of relative abundance reflect the corresponding patterns on the population level only if the proportion of sampled individuals remains the same over time. However, that applies only if there is a pattern in the change of the sampled proportion. If the variation is randomly distributed, it constitutes only an inefficiency of measurement, increasing the stochasticity (Link & Sauer 1998) hence the introduction of the random year effect into the modeling (Knappe 2016).

For instance, when the year effect was considered in the analysis, four out of five trends reported in Seibold's study became non-significant. They remained similar in their direction and intensity but with much higher uncertainty. With decreasing sample sizes, prominently in short-term studies, the sampling error and random variation contribute more to the strength of detected trends. That is one of the reasons why short studies report the most dramatic, both declining and increasing trends (Daskalova *et al.* 2021).

As Knappe (2016) demonstrates, the main risk when ignoring the random year effect is the inflation of p-values in long-term trends. Traditionally trends were modeled as *linear* trends in abundance. Now it is common to model non-linear trends that can reveal more about the population change. They allow conservational biologists to detect recent declines and are not so sensitive to the time window chosen for analysis (Knappe 2016). That is useful as analysis of long-span data may report a long steady trend masking over more short-term trends, which may change the perception of the population change (e.g., Crossley *et al.* 2020; see also van Klink *et al.* 2020b).

Especially in large-scale monitoring programs, there are many sources of random variation, changes in sampling method, observers, differences among the sites (Gaston & McArdle 1994). Therefore, it is essential for a statistical analysis to reliably estimate the degree of uncertainty (Link & Sauer 1998) to find out how representative of the population are the samples. Ignoring the random temporal year-effect may result in a significant shift of the distribution of p-values with an accent on the low end when estimating long-term trends. This will prevent substantiated decisions about the significance of the results and exacerbate the risk of type I error (Knape 2016).

3.2.6 Temporal scale

While we mentioned the importance of the study duration and the number of evaluated time points, the temporal scale of detected trends was overlooked. In the vast majority of studies, long-term linear trends are derived from the models, hopefully allowing compelling predictions, but recently fitting non-linear models gained traction (Knape 2016). Macgregor *et al.* (2019) demonstrated how segmented regression on a fractional scale permitted detection of initially increasing trend followed by a less dramatic decline. Høye *et al.* (2021) show how the resolution impacts the perceived dynamic. Had they used segmented regression in their previous study, they would find an abrupt change in the population trend. They eventually detected the changing direction of the trend in the more recent study when they fitted non-linear trends with better resolution.

3.2.7 Inter-annual timing and phenological shifts

Due consideration should be dedicated to the period in which the sampling is carried out each year. Phenological shifts must be accounted for in the study design. In insects, long-term monitoring with a fixed date of sampling will likely not accurately reflect the population properties (Bell *et al.* 2015; Møller 2019; Gardiner & Didham 2020) because insects partition themselves not only horizontally and vertically in space but also in time. The need to account for the phenological shifts throughout the year intensifies with long-term studies and if the sampling is carried out in a relatively narrow time window every year. If dynamic is not accounted for, detected trends may not be comparable to previous measurements as they are results of monitoring in a moment when insect activity is not optimal (Hodgson *et al.* 2011; Didham *et al.* 2020).

3.3 The sampling method

The final fundamental element of the study's methodology, which determines its information content, is the sampling method (Isaac & Pocock 2015). The selected method must, above all, reflect the taxonomical or functional target group of the survey and, occasionally, the season of the study (Saunders *et al.* 2020a; Santos *et al.* 2021). Every way of sampling is biased toward some specific taxa and has its benefits and limitations. The particularities and biases of the different sampling methods are beyond the scope of this work. We mention some general considerations that have the potential to influence the credibility and interpretation of the results.

3.3.1 Taxonomical resolution

Naturally, the critical step is to choose what group of species are the target of our study, whether it is flying insects in general, hymenoptera, wild bees, or just one particular species. That will determine what localities and habitats the survey will concentrate on, when the sampling will happen, and what specimen collection methods will be employed. Then we must consider the allocation of our efforts, distribute our resources among spatial and temporal replications and choose a suitable taxonomical scale to maximize the efficiency of our analysis. The details will largely depend on our approach. If we aim to extrapolate the results onto a larger geographic scale, we will maximize the number of spatial replications. Detecting the most robust trends largely independent of short-term fluctuation will require numerous temporal replications. Sensitive detection of species-specific population trends will then call for fine taxonomical resolution and individual identification.

Some well-known taxa, such as butterflies, have been proposed to serve as indicators or proxies for other insect groups, but only if thoroughly substantiated. (Thomas 2005, but see Hambler & Speight 2004; Henry *et al.* 2019). However, available studies show that a change in one taxonomic group does not mean a corresponding change in other taxa, and the same goes for species (Biesmeijer *et al.* 2006; Brooks *et al.* 2012; Oberprieler *et al.* 2020; Yong *et al.* 2020). Similarly, as we demonstrated earlier, abundance measured on a higher taxonomical level is not a good proxy for dynamics on a finer taxonomical scale (Høye *et al.* 2021). Examination of species-specific trends combined with trait analysis can help to understand the biological reasons behind the changes. Values measured on the higher taxonomical level may also mask over even dramatic community composition changes (Bokhorst *et al.* 2012).

One of the impediments of species-level examination is that we do not know as many as 80% of insect species (Stork 2018). The studies are often focused on the well-known taxa resulting in a phylogenetic and functional bias. For example, pollinators were the subject of several funding initiatives, and therefore there is much more data for a relatively small portion of the tree of life (Cardoso & Leather 2019). The baseline knowledge is so poor that butterflies are often the only insect taxa for which an accurate measure of change can be obtained (Thomas 2005).

The second obstacle is that in species-rich areas or with a high sample size, it can be time and cost-prohibitive to classify the specimen (Montgomery *et al.* 2020). Hallmann *et al.* (2021) had to go through almost 20,000 hoverfly specimens to classify just two years' worth of samples from 6 malaise traps. Høye *et al.* (2021) mention what a hurdle taxonomical identification is, point out its unreliability, and hope for new genetic methods to complement the traditional approach. More authors expect the genetic and other modern methods to give entomologists a helping hand (Saunders *et al.* 2020a). Notably, genetic identification (Pons *et al.* 2006; Renaud *et al.* 2012a) and environmental DNA (eDNA) hold much promise (Shaw *et al.* 2017). The genetic methods also pose their challenges, including needed expertise, elevated costs (Hunter *et al.* 2018), and, as far as eDNA is concerned, a library of known species with their respective markers (Deiner *et al.* 2017).

Timms *et al.* (2013) hypothesize that encountered discrepancies of their result with another study (Fernandez-Triana *et al.* 2011) arose due to the barcoding identification that the latter study used. Fernandez-

Triana *et al.* reported new species that might have been very closely related to those which initially lived at the examined location with changes in the employed genetic markers. The barcoding method might have been too sensitive and overreported new species.

Finally, several authors mention their concerns about the state of entomological taxonomy (Leather 2009; Cardoso *et al.* 2011; Saunders *et al.* 2020a). According to some, a taxonomy crisis is outlining as the numbers of taxonomists decrease, the entire field is underrepresented in university programs and generally underfunded (Leather 2009). With every retiring taxonomist, a great deal of information is lost, and a replacement is often lacking (Hopkins & Freckleton 2002).

To address these impediments, a simplified approach is often adopted, and only the easier quantifiers like biomass or aggregate abundance data are used for the analysis (e.g., Hallmann *et al.* 2020), even though species identification is necessary to understand the true nature of the changes (Cardoso & Leather 2019; e.g., Hallmann *et al.* 2021).

3.3.2 Method standardization

The pervasive lack of knowledge and the filling of gaps are further complicated by the prevailing lack of method standardization. Most of the mentioned biases can be prevented or commonly assessed, quantified, and filtered out if scientists use standardized methodology. Standardization is the most pressing issue on the agenda, as only consistent use of standardized methods can provide interoperable data. Hypothetically, we need data to infer large-scale trends while being able to zoom down to the local population level with a species-specific resolution and all of that continuously in time.

In Britain, for example, comprehensive datasets are collected by a network of instructed volunteers gathering valuable data using standardized light traps or so-called Pollard walks. The large-scale monitoring programs producing data that meet most of these requirements proved helpful while reporting robust trends on different time scales, but they have limitations. For instance, the RIS light traps yield small sample sizes, making the network statistically reliable only for widespread and common species (Conrad *et al.* 2004). The Pollard walk protocol of sampling transects is valid only for large, well-known species which are identifiable on the go or easily enough trapped with an entomological net (Montgomery *et al.* 2021).

Furthermore, examining long linear trends tells us little about the underlying biological processes. Conrad *et al.* emphasize the importance of short-term hypothesis-driven research (Conrad *et al.* 2004). Others agree that establishing new large centralized monitoring programs is not the only priority (Cardoso & Leather 2019; Wepprich *et al.* 2019). Some warn that if done wrong, large-scale monitoring can get very costly and ineffective (Tepedino *et al.* 2015; Cardoso & Leather 2019; Saunders *et al.* 2020a). Making historical and opportunistic data accessible and interoperable between different analyses could help integrate all available information sources. (Pagel *et al.* 2014; Dennis *et al.* 2017).

Nevertheless, standardization within large-scale monitoring schemes retains strong support (Conrad *et al.* 2007; Navarro *et al.* 2017; Eisenhauer *et al.* 2019; Montgomery *et al.* 2020, 2021) as they produce comprehensive output (Conrad *et al.* 2002, 2004, 2006; Shortall *et al.* 2009; Bell *et al.* 2015, 2020; Macgregor

et al. 2019). Long-term programs also face challenges of funding, and it is worth mentioning some of the pitfalls. Funding is usually organized at the national level, which can contribute to the fragmentation of the monitoring initiatives. Therefore, organizations and institutions on the international level should be employed (e.g., the EU). Another problem is that science funding is often awarded on a short-term basis, making stable monitoring programs with more substantial initial investments of time, work, and money risky and generally unsustainable (Cardoso & Leather 2019). That is why in some regions, most of the data is eventually collected by various entomological societies whose members are often volunteers (e.g., Conrad *et al.* 2004; Vogel 2017) or museums that are funded in a different more stable manner. That is why the envisaged consistent monitoring programs should be established as a core work of a university, museum, or NGO (Cardoso & Leather 2019)

Overall, the utmost priority is standardization, whether it is part of an extensive monitoring scheme or individual research. Standardization makes data interoperable, allows repetition of the experiment and confirmation possible, and can facilitate easier upscaling of the monitoring effort across the globe with little investment (Cardoso & Leather 2019).

Loboda *et al.* (2018) demonstrate how the consistent sampling protocol allowed them to detect and explain the change in the composition of diptera assemblages caused by shifts in the relative abundance of some species. At the same time, other similar studies could not detect these changes because of shortcomings in the methodology (Renaud *et al.* 2012b; Timms *et al.* 2013).

3.3.3 Sampling bias

Suppose we are to rely on the measured data when making extrapolations to population levels. In that case, we must be sure that the results of our individual sampled subpopulations closely resemble the trends and dynamics of the global population. Risks and complications of the temporal and spatial design were already discussed but we did not consider the detection aspects.

What are the consequences if the variation in the abundance of the obtained samples does not reflect the variation in the global population? In insects, it is rarely possible to census a whole population, so standardized methods must be employed to ensure a consistent and accurate representation of reality. Another issue is that most insect monitoring methods measure the insect's activity rate instead of abundance. All of the usual methods have various biases (Isaac & Pocock 2015; Didham *et al.* 2020) that are not necessarily problematic as long as they are dispersed randomly from the perspective of the spatial and temporal trends we try to explore (Link & Sauer 1998). A problem arises when the detectability of individuals changes based on abiotic factors, which results in altered perceived (sampled) abundance without any foundation in the population's dynamics (Didham *et al.* 2020). A bias may occur when various species' detectability significantly differs (Hallmann *et al.* 2020). Didham formulates several effects that might influence the credibility of sampling.

One example is when the chance of detection changes based on environmental conditions, e.g., insect activity rate depending on the weather without reflecting their actual abundance. Didham provides an example that he hypothesized in his previous study of the glow-worm population in England (Gardiner & Didham 2020).

Detectability might also be affected by human alteration of the environment, e.g., artificial light pollution could result in lower detection of glowing female glow-worms in transect counting surveys (Didham *et al.* 2020; Gardiner & Didham 2020). Additionally, artificial light sources might present a competing light source for the females that must attract the males by bioluminescence to mate successfully. That can have a tangible impact on the population if the reproduction rate declines because of courtship being hindered by the artificial lighting (Ineichen & Rüttimann 2012; Gardiner & Didham 2020; Owens *et al.* 2020). It can also bias a potential survey as the females who did not mate successfully will not stop glowing and will be accumulating with the later hatched females resulting in high counts of glowing females even though they might not mate. If we use the number of glowing females as a proxy for population abundance, such counts report precisely the opposite trend in the population. The authors make sure to reflect this in the interpretation of their glow-worm survey (Gardiner & Didham 2020) and report a decline in *sample* abundance.

The second case considers attraction-based trapping that loses its effectivity when similarly stimulating attractants are present, e.g., intense light pollution when catching moths with light traps (Didham *et al.* 2020). Even more significant decline in sample abundance could be caused by a competing attractant that is accompanied by increased mortality. For instance, moths are in greater danger near street lamps, where they can die of a collision, overheating, dehydration, or be hunted by bats (Owens & Lewis 2018; Owens *et al.* 2020). The detectability plummets, and so does the sample abundance. The increased mortality of light-seeking species near artificial light sources at night, which work as ecological traps, exerts intense selection pressure. This pressure can suppress light-seeking behavior (Altermatt & Ebert 2016) and, therefore, decrease the detectability of such species with light traps (Didham *et al.* 2020).

A similar but somewhat opposite effect occurs when attracting insects on a bait containing or mimicking a resource that is temporarily unusually scarce in the environment. That will result in inflated sample abundance (Didham *et al.* 2020), e.g., increased detection of pollinators during years of flower scarcity (Baum & Wallen 2011).

Furthermore, the scale and frequency at which insects are sampled must be considered. Disproportionate sampling may result in a partial depletion of populations, resulting in a perceived drop in abundance. This risk is, on average, the least imminent (Minteer *et al.* 2014; Gezon *et al.* 2015) but should be mentioned particularly in connection to monitoring rare species (Ward *et al.* 2001; Didham *et al.* 2020). Recently in connection to this problem, a large-scale monitoring program proposal (Lebuhn *et al.* 2013) was criticized for the number of bees and other non-target invertebrates that would fall victim to this survey (Tepedino *et al.* 2015). Large-scale non-selective sampling must also be considered from an ethical perspective, as both public and scientific ethical standards evolve (Drinkwater *et al.* 2019).

Finally, an issue closely connected to detectability is that those sampling methods that rely on catching insects when they are moving provide information about the insect's activity rate rather than abundance. That makes extrapolation to the global population harder if we consider that the mobility and dispersal rate of insects might depend on the population density. Høye *et al.* (2021) demonstrate how the density of some arthropod species was more explanatory than the hypothesized predictor. Suppose the individuals in a dense population

are driven to disperse into less densely populated habitats or actively seek new resources. In that case, they will be more susceptible to get trapped as they will more often leave their cover and travel through open space. This effect will result in inflated abundance reports in population peak and underestimated in population trough if not considered.

4 Conclusion

Based on the presented review, what do we *know* about insect decline? Can we conclude that insects are in trouble? We established that insect decline is relative to the measured parameter. “Insect decline” is an ambiguous term and can describe any of the nonequivalent declines in biomass, abundance, diversity, or reduction in geographical range. There is substantial evidence of declines in various metrics, some of which we summarized here. Nevertheless, if one wants to know about general insect decline, analyses of multiple metrics are needed (Habel *et al.* 2019) over a wide spatial and taxonomical range.

There is still not enough available data to provide definite answers; however, some attempts have been made to remedy that. We have already mentioned the meta-analysis by van Klink *et al.* (2020b) which currently presents the most comprehensive insect decline analysis. The authors reported a mean decline in abundance (including a limited number of studies reporting biomass) of terrestrial insects by ~9% per decade and an increase of freshwater insects by ~11% per decade.

The authors of the controversial and heavily criticized review from 2019, Sánchez-Bayo and Wyckhuys, recently published additional evidence for insect decline (Sánchez-Bayo & Wyckhuys 2021). They focused on long-term studies and drew upon additional datasets, including studies from Greenland, northern Africa, South America, eastern Asia, and Australia, to complement the predominant studies from Europe and North America. They report that 37% of species in the ten major insect orders are declining in numbers while 18% are increasing, even though the nature of the results makes interpretation difficult. In contrast to van Klink *et al.*, Sánchez-Bayo and Wyckhus concluded that 42% of species in aquatic communities are declining, and 29% are increasing.

There is an ongoing need for more data to facilitate similar large-scale analyses. Scientists largely agree that one of the most pressing problems is the lack of method standardization and data interoperability (Cardoso *et al.* 2011; Montgomery *et al.* 2021). Standardization is not the only challenge. The varying quality of entomological data often pushes the researchers to the limit, whether it is the survey design or the subsequent analysis. As we demonstrate, every study has to tackle many obstacles arising from the complexity of insect ecology and overcome the risks of bias. It is also the elimination of bias in the studies that allows the interoperability of data.

Scientists should harmonize their methods, so the ongoing monitoring initiatives head towards a common goal (Montgomery *et al.* 2021). Simultaneously, individual studies that are usually very limited, both geographically and taxonomically, should aspire to create a network of monitoring programs with aligned practices and complementary results. Centralizing tendencies sporadically appear, but before the efforts can be aggregated, there needs to be a harmonization of methods and metadata on an individual basis. Without

alignment, synchronization is impossible, and the data produced by the many researchers across the world will remain incompatible.

The available data permits the conclusion that insects are declining, whether it is in numbers or in diversity. Notwithstanding that, the details of the decline, for instance, the geographical and taxonomical range and its intensity in the less investigated parts of the planet, are still largely covered by the veil of uncertainty (Montgomery *et al.* 2020).

Finally, the most general issue is that, in many cases, due to lousy baseline data, flawed design, or insufficient sampling, we do not know the true level of uncertainty. As Knape (2016) demonstrates, the p-values are reliable only when the experiment and analysis are designed correctly. Therefore, it is also essential to report the amount of explained variability and attach confidence intervals to the models.

Furthermore, scientists should not be worried about communicating results that do not bring definite answers. The incapability of communicating the uncertainty may send a wrong message to the public and policymakers. The answer to a vast majority of questions concerning insect population trends is that we still do not know yet. In an ideal world, the uncertainty would be an impulse provoking research initiatives and attracting funding. As the uncertainty may not have the leverage on the decision-makers, science must ensure that its primary instrument, providing evidence, remains trusted and trustworthy by providing information based on robust data analysis and self-critically evaluating the uncertainty of reports.

Furthermore, suppose the insect decline is prematurely communicated and accepted due to failure to communicate the uncertainty of the issue (Saunders *et al.* 2020a). In that case, a confirmation bias (Nickerson 1998) will affect the character of the undertaken studies, which could have a deteriorating effect on future research (Montgomery *et al.* 2020). It is also important to remember that studies reporting dramatic results are more likely to be published. In fields with a small number of surveys, the probability of claims being true is reduced (Ioannidis 2005), which is concerning, especially when considering that studies about insects are much less likely to be published than studies concerning other taxa (Leather 2009) which further reduces their amount. Generally, the situation should be approached very critically, as this form of publication bias might be at play (Rosenthal 1979). It is also important to actively prevent the effects of publication bias and conscientiously publish reports of stable and increasing trends. It is vital for removing bias from future meta-analyses that can bring together large quantities of various studies and, to some extent, supplement large monitoring programs (Montgomery *et al.* 2020, 2021).

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