



UNIVERSITY OF LEEDS

This is a repository copy of *Interpreting insect declines: seven challenges and a way forward*.

White Rose Research Online URL for this paper:
<http://eprints.whiterose.ac.uk/159088/>

Version: Accepted Version

Article:

Didham, RK, Basset, Y, Collins, CM et al. (10 more authors) (2020) Interpreting insect declines: seven challenges and a way forward. *Insect Conservation and Diversity*, 13 (2). pp. 103-114. ISSN 1752-458X

<https://doi.org/10.1111/icad.12408>

© 2020, The Royal Entomological Society. This is the peer reviewed version of the following article: Didham, RK, Basset, Y, Collins, CM et al. (10 more authors) (2020) Interpreting insect declines: seven challenges and a way forward. *Insect Conservation and Diversity*, 13 (2). pp. 103-114. ISSN 1752-458X, which has been published in final form at <https://doi.org/10.1111/icad.12408>. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Use of Self-Archived Versions.

Reuse

Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

Takedown

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.



eprints@whiterose.ac.uk
<https://eprints.whiterose.ac.uk/>

1 **SPECIAL ISSUE**

2 **Interpreting insect declines: seven challenges and a way forward**

3

4 RAPHAEL K. DIDHAM^{1,2}, YVES BASSET^{3,4,5,6}, C. MATILDA COLLINS⁷, SIMON R.

5 LEATHER⁸, NICK A. LITTLEWOOD⁹, MYLES H. M. MENZ^{1,10,11,12}, JÖRG

6 MÜLLER^{13,14}, LAURENCE PACKER¹⁵, MANU E. SAUNDERS¹⁶, KARSTEN

7 SCHÖNROGGE¹⁷, ALAN J. A. STEWART¹⁸, STEPHEN P. YANOVIK^{3,19} and

8 CHRISTOPHER HASSALL²⁰

9

10 ¹School of Biological Sciences, The University of Western Australia, Crawley WA 6009, Australia

11 ²CSIRO Health & Biosecurity, Centre for Environment and Life Sciences, Floreat WA 6014, Australia

12 ³Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Panamá.

13 ⁴Faculty of Science, University of South Bohemia, 370 05 Ceske Budejovice, Czech Republic

14 ⁵Biology Centre of the Czech Academy of Sciences, Institute of Entomology, 370 05 Ceske Budejovice, Czech

15 Republic

16 ⁶Maestria de Entomologia, Universidad de Panamá, 080814 Panama City, Republic of Panama

17 ⁷Centre for Environmental Policy, Imperial College London, The Weeks Building, 16-18 Princes Gardens,

18 London SW7 1NE, UK

19 ⁷Department of Crop & Environment Sciences, Harper Adams University, Edgmond Newport, Shropshire TF10

20 8NB, UK

21 ⁹Department of Rural Land Use, SRUC, Ferguson Building, Craibstone Estate, Bucksburn, Aberdeen AB21

22 9YA, UK

23 ¹⁰Department of Migration, Max Planck Institute of Animal Behavior, Radolfzell, Germany

24 ¹¹Centre for the Advanced Study of Collective Behaviour, University of Konstanz, Konstanz, Germany

25 ¹²Department of Biology, University of Konstanz, Konstanz, Germany

26 ¹³Field Station Fabrikschleichach, Department of Animal Ecology and Tropical Biology, Biocenter, University

27 of Würzburg, Glashüttenstraße 5, 96181 Rahenebrach, Germany

28 ¹⁴Bavarian Forest National Park, Freyunger Str. 2, 94481 Grafenau, Germany

29 ¹⁵Department of Biology, York University, 4700 Keele St., ON, M3J 1P3, Canada

30 ¹⁶School of Environmental & Rural Science, University of New England, Armidale NSW Australia

31 ¹⁷UK Centre for Ecology & Hydrology, Wallingford OX10 8BB, UK

32 ¹⁸School of Life Sciences, University of Sussex, Falmer, Brighton BN1 9QG, UK

33 ¹⁹Department of Biology, University of Louisville, 139 Life Sciences Building, Louisville, KY 40292, USA

34 ²⁰School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds, UK

35

36 **Running title:** Interpreting insect declines

37

38 **Abstract**

39 1. Many insect species are under threat from the anthropogenic drivers of global change.

40 There have been numerous well-documented examples of insect population declines and
41 extinctions in the scientific literature, but recent weaker studies making extreme claims of a
42 global crisis have drawn widespread media coverage and brought unprecedented public
43 attention. This spotlight might be a double-edged sword if the veracity of alarmist ‘insect
44 decline’ statements do not stand up to close scrutiny.

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

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

54 4. Despite many existing challenges and pitfalls, we present a forward-looking prospectus for
55 the future of insect population monitoring, highlighting opportunities for more creative
56 exploitation of existing baseline data, technological advances in sampling and novel
57 computational approaches. Entomologists cannot tackle these challenges alone, and it is only
58 through collaboration with citizen scientists, other research scientists in many disciplines, and
59 data analysts that the next generation of researchers will bridge the gap between little bugs
60 and big data.

61

62 **Keywords:** citizen science, detection bias, global insect decline, insect conservation,
63 monitoring, phenological shift, population trend, sampling bias, shifting baseline, time series

64

65 **Introduction**

66 Populations of many insect species are declining (Wagner, 2020). For the vanishingly small
67 proportion of these in which conservation risk has been evaluated (e.g., Langor 2019), the
68 status and trends are at least as sobering as they are for vertebrate species (Dirzo *et al.*, 2014;
69 Forister *et al.*, 2019). This will, of course, come as no surprise to entomologists, who have
70 been reading about declining insect populations in *Insect Conservation and Diversity*, among
71 other journals, for at least a decade (e.g., Shortall *et al.*, 2009; Fox, 2013; Cardoso & Leather,
72 2019). For the general public, however, it has come as an alarming revelation, brought to the
73 fore by several recent studies that received worldwide media attention (e.g., Hallmann *et al.*,
74 2017; Lister & Garcia, 2018; Sánchez-Bayo & Wyckhuys, 2019). The quality of some of
75 these papers has been relatively weak, either due to misinterpretation of data (Lister &
76 Garcia, 2018) or overzealous claims (Sánchez-Bayo & Wyckhuys, 2019). The scientific
77 response to this has been an exemplar of the nature of science as a self-correcting endeavour,
78 with critical re-evaluation of the findings emerging rapidly (e.g., Willig *et al.*, 2019; Cardoso

79 & Leather, 2019; Cardoso *et al.*, 2019; Komonen *et al.*, 2019; Montgomery *et al.*, 2019;
80 Mupepele *et al.*, 2019; Simmons *et al.*, 2019; Thomas *et al.*, 2019; Wagner, 2019; Saunders
81 *et al.*, 2020a). The global media response has been something entirely different, but has put
82 insect conservation firmly on the public and policy agenda (Harvey *et al.*, 2020). As Cardoso
83 *et al.* (2019) and Montgomery *et al.* (2019) point out, though, this spotlight could become a
84 double-edged sword as the veracity of the more alarmist ‘insect decline’ statements faces
85 increased scrutiny.

86 In the rush to address ‘global insect declines’, it has never been more important to
87 pause and think critically about what constitutes evidence for decline in the first place. For
88 most insects, high inter-annual variability is the norm rather than the exception, (e.g.,
89 Redfearn & Pimm, 1988; Roubik, 2001), but it poses serious problems in determining what
90 the baseline ‘reference state’ should be for historical abundance, and inherently increases the
91 length of time series required to separate signal from noise (White, 2019). Any number of
92 artefacts in the data compilation, analysis or interpretation of the findings could also result in
93 an apparent change from presence to absence or high to low abundance between two time
94 points, without there necessarily being a significant trajectory of decline in population size
95 through time. Here, we identify seven key problems in quantitative inference about insect
96 declines, grouped loosely as errors of baseline, trend estimation and resulting population
97 inference. This is not intended to be a comprehensive review of the subject, but rather a
98 framework for approaching the broad and growing literature on insect population trends
99 through time, with selected examples to illustrate key challenges in inferring a decline in
100 abundance. The seven problems we identify are not intended to be mutually exclusive either,
101 and there will be substantial conceptual overlap in how they are dealt with and resolved. We
102 conclude by presenting guidelines for best-practice approaches to mitigate bias, and a

103 forward-looking prospectus for the future of insect monitoring, aimed at an up-and-coming
104 generation of researchers who can bridge the gap between little bugs and big data.

105

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

126 In the absence of long time series of decline, many studies use a haphazard assortment
127 of historical data as proxies for the missing baseline (Bonebrake *et al.*, 2010), but despite

128 these often being all that we have, they are rarely likely to be fit for purpose. For instance,
129 historical quantitative surveys might have been designed to address an unrelated ecological
130 question, and therefore (inadvertently) violate the statistical assumptions needed to produce
131 an unbiased estimate of historical population abundance. Using data simulations, Fournier *et*
132 *al.* (2019) describe how non-random site selection bias in the measurement of historical
133 baseline conditions could significantly increase the probability of inferring a false decline,
134 even when there is no long-term trend in the data. This (they argue) is because researchers are
135 much more likely to select sites where their study organisms are known to occur, and/or are
136 sufficiently abundant to sample. Plausibly, an above-average starting point in a time series
137 comparison – a ‘false baseline effect’ (Figure 1) – could lead to an apparent decline through
138 time as a simple statistical artefact of regression to the mean, especially when abundances are
139 fluctuating widely from year to year (Fournier *et al.*, 2019).

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

144

145 **The missing zero effect** – The corollary of site-selection bias inflating average local
146 abundance at baseline, is that unoccupied sites (i.e., true absences, not detection errors) will
147 be under-represented in local population estimates. Assuming that these unoccupied sites are
148 potentially occupiable (i.e., represent suitable habitat, linked by dispersal, in some sort of
149 spatially-structured population context; Hanski, 1998; Ovaskainen & Saastamoinen, 2018),
150 then rates of decline will be over-estimated at the local sites where abundances are measured,
151 and unrepresentative of the wider sampling universe of potentially occupiable habitat. We
152 call this the ‘missing zero’ effect, after the wonderful children’s mathematics book *Nesta and*

153 *the Missing Zero* (Leibrich, 2006) in which the loss of ‘nothing’ throws the world into chaos.
154 Local populations might well be declining at known sites with high historical abundance, but
155 other local populations could be increasing (concurrently) at formerly unoccupied or
156 unsampled sites, especially if there are density-dependent feedbacks on intrinsic rates of
157 population increase or asynchronous dynamics among local subpopulations (Pollard, 1991;
158 Sutcliffe *et al.*, 1996).

159 At local scales, the missing zero effect squanders the opportunity to measure future
160 recolonisation of unoccupied sites, through (i) natural processes associated with spatially-
161 structured population dynamics (Ovaskainen & Saastamoinen, 2018; Dallas *et al.*, 2020), (ii)
162 rehabilitation of sites following mitigation of threatening processes (e.g., Corlett, 2016;
163 Pilotto *et al.*, 2018), or (iii) as a result of extra-limital processes such as shifting geographic
164 ranges due to climate change and species invasion (e.g., Walther *et al.*, 2009; Hill *et al.*,
165 2012; Hill *et al.*, 2017; Rabl *et al.*, 2017). At the regional scale, missing zeros are also the
166 connection between local abundance measures and regional occupancy changes, with which
167 we deal separately below.

168
169 **The snapshot effect** – Estimates of population change can be sensitive to selection bias
170 effects in the choice of contemporary time-points, much as described for false baseline effects
171 above. In the simplest case (i.e., a pairwise ‘snapshot’ comparison of historical versus
172 contemporary populations; Figure 1), there is high potential for time-selection bias in
173 contemporary estimates. Anecdotal reminiscing about how ‘numbers are not what they used
174 to be’ (e.g., Vogel, 2017) could easily lead to ‘confirmation bias’ in the choice of a single
175 contemporary time-point where numbers are substantially lower than average contemporary
176 conditions (e.g., Figure 1). The motivation for selecting a particular time-point for
177 comparison, and knowledge of fluctuations in the intervening years, are fundamentally

178 important considerations in evaluating snapshot data (*viz* criticisms about the Lister & Garcia,
179 2018 study).

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

202 Fournier *et al.* (2019) suggest that left-censoring of time series (Figure 1) can be a
203 useful approach to detect and overcome potential false baseline effects (effectively a
204 sensitivity test of whether the trend slope remains unchanged with progressive removal of
205 early time points in the time series). They found that false baseline effects over-estimated
206 decline slopes most substantially in time series with fewer than 10 time points (Fournier *et*
207 *al.*, 2019). The same logic could potentially be used for right-censoring short time series to
208 overcome bias in contemporary snapshot effects (Figure 1). Framing the combination of the
209 two approaches more generally, a walk-forward cross-validation or combinatorial k-fold
210 cross-validation procedure for time series (e.g., Bergmeir *et al.*, 2018) could be used to
211 determine sensitivity to outliers in the data, when time series are shorter than the 15 time
212 points recommended by White (2019).

213 A salient example of just how important cross-validation could be, is the recent study
214 of arthropod decline in Germany over a 10-year time series from 2008-2017 (Seibold *et al.*,
215 2019). The overall time series trend, as well as region-specific and taxon-specific trends, are
216 heavily influenced by one or two time-points in the data (see Fig. 1 and Fig. S3-1 in Seibold
217 *et al.*, 2019). To their credit, the authors attempt a sensitivity analysis by dropping one year of
218 the time series at a time, which “showed that the decline was influenced by, but not solely
219 dependent on, high numbers of arthropods in 2008” (Seibold *et al.*, 2019, p.672). This is
220 equivalent to a very shallow left-censoring of the time series in the case of the 2008 data
221 point, which (by visual inspection of the evidence in Seibold *et al.*, 2019) will have removed
222 a large component of the apparent trends, by itself alone. A full cross-validation would
223 certainly nullify any remaining evidence for a general decline trend in their data. This is not
224 to say that such a decline in arthropods is not occurring in these parts of Germany. The
225 decline may well be real, but at face value the data provide no indication whether abundance
226 in the next time-interval will be lower or higher than current estimates – and what is a time

227 series of decline for, if not to improve predictive power to understand future population
228 change?

229

230 **The detection bias effect** – All the arguments presented so far have assumed that variation in
231 sample abundance is an accurate representation of variation in local population abundance.

232 Unfortunately, few studies can achieve a complete census of all individuals in a population,
233 so it is a practical necessity in insect monitoring that standardised sampling methods are used
234 instead. Entomologists are well aware that most sampling methods measure activity rates not
235 population abundance, all methods have inherent biases, and different methods have different
236 biases that affect the accuracy of extrapolation to local abundance or population size
237 estimates (e.g., pitfall trapping: Baars, 1979; or pollinator monitoring: Westphal *et al.*, 2008).

238 Such biases are not necessarily problematic if their effects are randomly distributed with
239 respect to the spatial and temporal trends of interest. There are, however, a number of
240 potential processes that could result in temporal autocorrelation in the detectability of
241 individuals, such that abundance might appear to change through time simply because
242 individuals are becoming more or less detectable. It is this potential for temporal
243 autocorrelation in detectability that needs closer investigation. Here, we provide only a partial
244 (and cursory) set of examples of detection bias (for further examples see Isaac & Pocock,
245 2015), and there are likely to be many other situations in which temporal autocorrelation in
246 detectability might occur (setting aside the apocryphal ‘car windscreen design effect’, in
247 which declining insect splatter rates on cars could be due solely to the design of more
248 aerodynamic modern cars; Vogel, 2017).

249 A ‘detection effect’ might operate if the ability to capture or census individuals
250 changes with ambient environmental conditions (regardless of their actual abundance). The
251 most obvious example of this is that insect activity rates (and therefore probability of

252 detection) depend on ambient weather conditions (which are also changing through time).
253 Detection can also change with increasing human alteration of other aspects of environmental
254 conditions, such as artificial lighting at night. One way to monitor populations of the glow-
255 worm, *Lampyris noctiluca* (Linnaeus, 1767) (Coleoptera: Lampyridae) is by counting the
256 numbers of glowing females per km of transect (Gardiner, 2007; Gardiner & Didham, 2020),
257 but an increase in the intensity, or a change in the spectrum, of ambient background lighting
258 through time (from street lights, for instance) could make it increasingly difficult to detect
259 females, even when present. This is further complicated by the possibility that male glow-
260 worms have difficulty finding females against artificial background lighting, which could
261 produce real population-level consequences over the longer term (Owens *et al.*, 2020; Alan
262 Stewart, pers. obs).

263 Plausibly, in attraction-based trapping a ‘dilution effect’ could occur if an attractive
264 stimulus from competing anthropogenic sources was itself increasing through time. For
265 example, light trapping is used as a standard method for sampling moths, but in many rapidly
266 urbanising areas the number of competing anthropogenic sources of light has been increasing
267 dramatically through time (Gaston *et al.*, 2015; Owens *et al.*, 2020). Thus, moth captures
268 might decline through time simply because individuals are attracted elsewhere and are not as
269 detectable in the monitoring traps. In principle, this is no different than the well-known
270 phenomenon that light traps catch more moths on dark moonless nights than during the full
271 moon, as a result of less competition from other light sources (McGeachie, 1989). There
272 might be a tendency to think of this as just an urban problem, but dilution effects could affect
273 populations far from urban centers if artificial lighting affects regional dispersal. Such effects
274 are not known for artificial lighting, but in agroecosystems, landscape-scale dilution effects
275 from mass-flowering crops have caused reductions in the local capture rate of pollinators
276 (Holzschuh *et al.*, 2011), without necessarily changing regional population size. Naturally,

277 the converse ‘concentration effects’ from attraction-based trapping could plausibly occur as
278 well, if there is temporal covariance between lower ambient resource attraction in the
279 environment and consequent increased attraction to the baited trap, even if local population
280 size does not change (for instance, in baited pitfall trapping for dung beetles during years of
281 low dung availability, pheromone trapping for bark beetles when attractive volatile signals
282 from host trees are low, or coloured pan trapping for bees during years of floral scarcity; e.g.,
283 Baum & Wallen, 2011).

284 If artificial stimulus effects, such as attraction to light, are also compounded by an
285 added component of source-sink dynamics in the potential mortality associated with the
286 stimulus, then this could be a driver of real declines in abundance, over and above dilution
287 effects (Minnaar *et al.*, 2015). For instance, mortality is thought to be substantially higher for
288 some species in artificially lit areas (e.g., where bat predation on moths is focused around
289 streetlamps; Owens *et al.*, 2020), imposing an extreme selection pressure on some local
290 populations. Ironically, this ‘selection effect’ could also make evolving moths harder and
291 harder to detect through time in light-trap monitoring surveys. For example, Altermatt &
292 Ebert (2016) reared *Yponomeuta cagnagella* (Hübner, 1813) moths from populations in light-
293 polluted versus dark-sky regions of France and Switzerland, and found that moths from high
294 light pollution areas had a significant (30%) reduction in flight-to-light behaviour. This type
295 of selection effect could result in an overestimate of apparent declines in population size, due
296 to increasing trap shyness through time.

297 Finally, apparent local declines in abundance could occur due to a ‘depletion effect’
298 from removal sampling (e.g., kill-trapping of insects) in species that have low intrinsic rates
299 of population increase and very low dispersal ability (e.g., large-bodied, flightless Carabidae
300 beetle species in pitfall trap sampling programmes; Ward *et al.*, 2001). The declines
301 themselves are ‘real’ at the local level, but driven by the monitoring programme and not other

302 ecological causes that the monitoring programme was designed to test. We stress that it is
303 unlikely for standardised quantitative monitoring programmes to cause population-wide
304 decline due to over-collection (e.g., Gezon *et al.*, 2015), although the potential risks to rare or
305 localized species should always be evaluated carefully. In the sense that local depletion
306 effects are unrepresentative of wider regional population changes, then this is a detection bias
307 issue that arises due to low recruitment rates into the sampled population prior to the next
308 sampling interval.

309

310 **The Andrewartha effect** – When baseline identification, site selection, trend estimation, and
311 detectability are all known to be unbiased, the natural temptation might be to infer that
312 sample estimates of decline equate directly to the real magnitude of population decline.
313 However, there are several reasons why caution is still needed in drawing population-level
314 inference.

315 The first reason is that many insect decline studies are founded on an implicit, but
316 untested, assumption that insect dispersal rates are density-independent. Many (perhaps most)
317 insect monitoring methods are based on detecting moving insects, such as beetles in pitfall
318 traps, wasps and flies in Malaise traps, or aphids in suction traps. Logically this means that
319 changes in sample abundance are only a good proxy for changes in population abundance if
320 activity rates are density-independent. The problem is that at high population densities the
321 frequency of dispersal events might be expected to increase in a density-dependent manner
322 (e.g., due to local resource limitation), while at lower population densities the frequency of
323 dispersal events might be expected to decline, and not necessarily in a linear manner (Denno
324 & Peterson 1995; Enfjäll & Leimar, 2005; Régnière & Nealis, 2019). If this is generally the
325 case, then movement-based monitoring techniques might overestimate population size at
326 peak abundance, and underestimate population size in population troughs, potentially

327 resulting in over-estimates of rates of decline as populations get smaller (as well as the
328 converse, as populations get larger). In rarer cases, the opposite pattern of negative density
329 dependence in dispersal rates has also been shown in some damselfly species with unusual
330 habitat requirements (Chaput-Bardy *et al.*, 2010), or where conspecifics are potentially used
331 as cues for habitat quality (Roquette & Thompson, 2007). In all of these cases, density-
332 dependence in insect movement rates is incompatible with a direct extrapolation from
333 declining sample abundance to declining population size. We call this the ‘Andrewartha
334 effect’ after the renowned Australian ecologist H.G. Andrewartha for whom density-
335 dependence was pure dogma, and all population processes were implicitly assumed to have a
336 density-independent basis until proven otherwise (Andrewartha, 1961).

337

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

352 sampling approach can be inappropriate in some circumstances (as recognised in the pest
353 management literature, where a degree-days approach is used), unless monitoring fully
354 brackets the phenological window and models adjust for inconsistency of environmental
355 responses through time (Gardiner & Didham, 2020).

356

357 **The popcorn effect** – A final potential problem in population-level inference is validating
358 the extent to which a small set of well measured local decline estimates can be extrapolated to
359 reduction in local and regional abundance patterns that might ultimately lead to population
360 extinction (in the extreme). In other words, the degree of covariance between local and
361 regional estimates of population change is typically unknown (but see Oliver *et al.*, 2017).
362 There is a tendency to take a few kernels of local data and expand these into a superficially-
363 inflated shell of population response as a whole. In consumer psychology, the ‘popcorn
364 effect’ is where a new phenomenon pops into a person’s mind and then that same
365 phenomenon appears to pop up everywhere, in a form of unconscious bias, as if it is a
366 generalised truth (also known as the frequency illusion effect, or Baader-Meinhof
367 phenomenon). In the context of population change, the popcorn effect could result in
368 misleading conclusions if there are substantial gaps in sample coverage of occupied versus
369 unoccupied areas (e.g., the ‘missing zero effect’ referred to above), such that local declines
370 are not representative of changes in either occupancy or average abundance across the region.

371 The correspondence between local decline estimates and regional occupancy trends
372 probably depends on the commonness or rarity of species sampled. From first principles, very
373 large local declines in aggregate measures of insect abundance, and to a certain extent
374 biomass (e.g., Hallmann *et al.*, 2017, 2020), must be driven predominantly by changes in the
375 abundance of common, rather than rare species (Shortall *et al.*, 2009). Thus, statistical
376 support for the local decline in abundance of common species is unlikely to correspond

377 directly to a decline in range-wide occupancy or increased risk of extinction (barring a few
378 celebrated examples, such as the extinction of the super-abundant Rocky Mountain locust
379 *Melanoplus spretus* Walsh, 1866, Orthoptera: Acrididae, Lockwood, 2010). By contrast, it
380 would be much more challenging to statistically ‘prove’ local declines in any of the rare
381 species in the aggregate samples. Yet in a comprehensive analysis of occupancy trends for
382 353 wild bee and hoverfly species in Great Britain from 1980-2013, Powney *et al.* (2019)
383 showed that it was precisely these rarer species that declined the most in occupancy through
384 time. There is of course the added complication that many occupancy studies, such as this,
385 use relative measures of population change (e.g., inferring absences from the presences of
386 other species in the same taxon). Equating relative population estimates to absolute
387 population changes is not necessarily straight-forward (for instance, if all species are
388 declining then such methods might fail to detect declines even though they are happening).

389 Both occupancy and abundance trends provide unique, and complementary, evidence
390 of declines, particularly if one is interested in the ecological or management implications of
391 population declines (Wepprich *et al.*, 2019). As Powney *et al.* (2019, p.3) state, “the lack of
392 standardized monitoring data limits our understanding of the link between change in species
393 occupancy, local abundance and [functional significance]” (pollination in their case). While
394 rare species can be of great conservation significance, they might tend to have relatively little
395 functional significance (in terms of contribution to ecosystem services such as pollination,
396 pest control and so on), compared with abundant species (e.g., Winfree *et al.*, 2015; but see
397 Dee *et al.*, 2019). Different management goals can require very different types of data and
398 different requirements in terms of designing robust monitoring programmes (e.g., for
399 pollination systems *cf.* LeBuhn *et al.*, 2013; Gallant *et al.*, 2014; and Bartholomé & Lavorel,
400 2019).

401

402 **A way forward**

403 Taken together, the seven potential challenges we have identified in accurately quantifying
404 time series trends in insect populations suggest that much greater care is needed in evaluating
405 the evidence for (and relative drivers of) declines. Equally, going forward, a number of key
406 recommendations will be important to consider in monitoring prospective time series of
407 recovery in insect populations following mitigation of threatening processes (Harvey *et al.*,
408 2020).

409 (i) Baseline estimation – Studies should explicitly state the limits to inference on their
410 selected ‘historical reference state’, in terms of time frame, representativeness of expected
411 past conditions, and the intrinsic magnitude of inter-annual fluctuations in population
412 abundance of the target species (as this determines the precision, accuracy and reliability of
413 forecasting and backcasting). More than one reference site (preferably many) should be
414 sampled to determine baseline conditions, when possible. Studies should consider site
415 selection bias when choosing these reference sites, with the aim of minimising or mitigating
416 non-random selection (including consideration of unoccupied, but potentially occupiable
417 sites), and in all cases should report site selection criteria in subsequent publications
418 (Fournier *et al.*, 2019). Where multiple data types and approaches are used to establish
419 baselines, the criteria for inclusion and integration should be transparent (Bonebrake *et al.*,
420 2010)

421 (ii) Trend estimation – Under most circumstances, time series ‘snapshot’ comparisons
422 between two time-points do not accurately reflect local abundance trends through time. At
423 best, these will only show a statistical difference between the two years sampled. Where these
424 pairwise snapshots could gain value in the future, however, is in the integration of many such
425 pairwise estimates at many sites over many time intervals, to build a composite time series of
426 evidence. For more robust direct measurements of population change, longer time series will

427 be needed. The minimum required length of time series depends on the magnitude of
428 temporal fluctuations in abundance (a signal to noise ratio issue), and we follow Fournier *et*
429 *al.* (2019) in suggesting that sampling artefacts in trend estimation decrease in time series
430 with more than 10 time-points, and White (2019) in suggesting that statistical power
431 increases in time series with more than 15 time-points. Cross-validation procedures (left-
432 censoring, leave-one-out cross validation against values with high leverage, and so on)
433 effectively determine sensitivity of the overall trend to outliers in the data. We also encourage
434 monitoring studies to standardise their presentation of population change estimates
435 (standardised effect sizes for rates of change per annum, through time) and lay their
436 predictive cards on the table by publishing forecast estimates in advance for the following
437 year(s), then testing the accuracy of the observed vs. predicted population trajectories.
438 Finally, given the intense demands on resources to support robust quantitative evaluation of
439 population trajectories, even at a relatively limited number of sampling locations, we
440 recommend that intensive monitoring programmes (typically 10-100 sites) conducted
441 annually (e.g., Karlsson *et al.*, 2020) are complemented by spatially extensive occupancy
442 surveys (e.g., 100-1000 sites) at less frequent intervals (e.g., every 3 – 5 years) perhaps using
443 citizen science programmes if data quality can be assured. The statistical bar for accurate,
444 precise and reliable estimation of regionwide occupancy trends through time will be
445 substantially lower (for most taxa) than it is for quantitative local abundance trends, making
446 occupancy data the logical target for citizen science monitoring.

447 (iii) Population inference – Studies using sampling methods in which the probability of
448 capture of each individual is not uniform through time (which applies to essentially all
449 quantitative insect sampling methods), should consider (and ideally test and report, where
450 possible) the effects of relevant detection bias effects, density-dependent variation in capture
451 probability, temporal covariance in the match between sampling period and insect activity

452 period, and the degree of covariance between local detection frequency and wider landscape-
453 level occupancy patterns and regional population size.

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

472 Despite many existing challenges and pitfalls, opportunities for creative exploitation
473 of existing baseline data (Bonebrake *et al.*, 2010; Habel *et al.*, 2019; Stepanian *et al.*, 2020)
474 and novel computational approaches (e.g., Outhwaite *et al.*, 2018) may resolve some issues.
475 Drawing inspiration from climate science, which has sought to describe trends and attribute
476 drivers in much the same way, researchers could attempt to cross-validate proxies for insect

477 abundance and diversity in overlapping time periods to create a coherent time series (Figure
478 2a). Tools for measuring population variation over time and accounting for complex
479 ecological information (Saunders *et al.*, 2019; Bahlai & Zipkin, 2020) already exist in
480 different fields such as paleoecology (e.g., Wilf *et al.*, 2001; Howard *et al.*, 2009), and
481 conservation genomics (Beichman *et al.*, 2018). Other emerging approaches, like using
482 machine learning to reverse-engineer the drivers of decline from empirical trends, may
483 dramatically improve analysis and interpretation (Martin *et al.*, 2018). The accessibility of
484 such advanced data science techniques for entomological researchers is increasing, including
485 through creative use of data science competitions to enhance inter-disciplinary collaboration
486 (Humphries *et al.*, 2018).

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

502 insect ‘noise’ from the meteorological signal in weather radar data can create a substantial,
503 standardised dataset for insect monitoring through time (e.g. Stepanian *et al.*, 2020). Further
504 advances in technologies such as LiDAR (light detection and ranging; Kirkeby *et al.*, 2016)
505 and camera transects (Ruczyński *et al.*, 2020) offer the prospect of new tools in the future. In
506 many cases, species-level identification can be a challenge with remote sensing methods, and
507 will require careful validation against conventional measures of insect population change
508 (e.g., Wotton *et al.*, 2019; Stepanian *et al.*, 2020) until further tools are developed, but they
509 show promise in helping to resolve some key issues in entomological data collection.

510 Finally, we encourage monitoring programmes to expand collaboration between
511 citizen scientists and researchers (e.g., MacPhail *et al.*, 2019), in spite of some caution that
512 has been raised about data quality, repeatability and taxonomic identification (Stribling *et al.*,
513 2008; Kremen *et al.*, 2011; Falk *et al.*, 2019). There may, however, be a need to revisit the
514 relative costs and benefits of different citizen science approaches (including the opportunities
515 and risks of integrating artificial intelligence; Wäldchen & Mäder, 2018; Ceccaroni *et al.*,
516 2019) in order to generate recommendations about which tools to adopt in insect population
517 monitoring. The goals of citizen science programs vary along a continuum from casual
518 engagement to intensive standardised data collection (e.g., Figure 2b), and effective citizen
519 science programs designed to monitor insect population trends should consider: (i) where
520 along that continuum is optimal for the scale and quality of data that are required, and (ii)
521 how best to support the citizen scientists who take part in such activities (training, rewards,
522 etc) (van der Wal *et al.*, 2016). Note that these data and analytical considerations are
523 inherently interlinked. Citizen scientists might help digitise museum collections to facilitate
524 phenotypic and genetic analysis, as well as deploy bioacoustics sensors. Researchers might
525 develop mathematical models that reveal previously unknown predictors which can then be
526 incorporated into future monitoring technologies. Radar technology might guide the design of

527 citizen science monitoring schemes through stratified sampling of landscapes. Only through
528 the full integration and cross-validation of these different data sources and approaches
529 (Figure 2a,b) will we be able to realise their full potential for monitoring insect population
530 trends.

531

532 **Conclusion**

533 We have made the case for a more critical approach to the study of ‘insect declines’ that
534 avoids methodological errors to produce a robust analysis of population trends through time
535 and the phenomena that drive them. We propose three key areas in which more focused
536 attention is needed: on baselines, trends, and population-level understanding. The future is
537 bright for insect monitoring, with new technologies coming online for the study of insect
538 abundance. However, the past remains dark due to the paucity of data. We suggest that
539 overcoming the lack of historical context will require collaboration across ecological and
540 statistical subdisciplines to share and cross-validate methods and datasets, in order to build a
541 much more robust composite time series of current trends. These quantitative considerations
542 are only part of the picture, of course, and may be a moot point if we do not reinforce the
543 importance of insects and their conservation on the public and policy agenda (Saunders *et al.*,
544 2020b). The recent media attention creates an exceptional opportunity for improved public
545 understanding, and for broader funding of insect research. Just as for other components of
546 biodiversity, raising the profile of insects and promoting a positive image may increase their
547 perceived value to a wider sector of society and pay dividends for future conservation and
548 restoration. A rich academic literature exists on the psychology and promotion of insects as
549 food and feed (van Huis, 2017; Collins *et al.*, 2019), for instance, and this type of ‘marketing’
550 approach applied to promoting the values of insects themselves could be a proactive way
551 forward for insect conservation (Hart & Sumner, 2020). Once we reinforce this social licence

552 to operate, we need to ensure that we have robust science to document ongoing trends and to
553 support future action.

554

555 **Acknowledgements**

556 We thank Sheila Colla, Laura Fagan, Clement Kent and Victoria MacPhail and the editorial
557 board at *Insect Conservation and Diversity* for useful discussion on the ideas presented here.

558 MHMM was supported in this project by funding received from the European Union's

559 Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant

560 agreement No. 795568. MES was supported by a University of New England Postdoctoral

561 Fellowship. KS was supported by UKRI (NEC06826).

562

563 **Conflict of Interest**

564 The authors declare no conflict of interest.

565

566 **References**

567 Altermatt F. & Ebert D. (2016) Reduced flight-to-light behaviour of moth populations

568 exposed to long-term urban light pollution. *Biology Letters*, **12**, 20160111

569 <http://dx.doi.org/10.1098/rsbl.2016.0111>.

570 Andrewartha, H.G. (1961) *Introduction to the Study of Animal Populations*. Methuen & Co.

571 Ltd, London, U.K.

572 Baars, M.A. (1979) Catches in pitfall traps in relation to mean densities of carabid beetles.

573 *Oecologia*, **41**, 25-46.

574 Bahlai, C.A. & Zipkin, E.F. (2020) The dynamic shift detector: an algorithm to identify

575 changes in parameter values governing populations. *PLoS Computational Biology*, **16**(1):

576 e1007542. <https://doi.org/10.1371/journal.pcbi.1007542>

- 577 Bartholomé, O. & Lavorel, S. (2019) Disentangling the diversity of definitions for the
578 pollination ecosystem service and associated estimation methods. *Ecological Indicators*,
579 **107**, DOI: 10.1016/j.ecolind.2019.105576.
- 580 Baum, K.A. & Wallen, K.E. (2011). Potential bias in pan trapping as a function of floral
581 abundance. *Journal of the Kansas Entomological Society*, **84**, 155-159.
- 582 Beichman, A.C., Huerta-Sanchez, E. & Lohmueller, K.E. (2018). Using genomic data to infer
583 historic population dynamics of nonmodel organisms. *Annual Review of Ecology,*
584 *Evolution, and Systematics*, **49**, 433-456.
- 585 Bergmeir, C., Hyndman, R.J. & Koo, B. (2018) A note on the validity of cross-validation for
586 evaluating autoregressive time series prediction. *Computational Statistics and Data*
587 *Analysis*, **120**, 70-83.
- 588 Bonebrake, T.C., Christensen, J., Boggs, C.L. & Ehrlich, P.R. (2010) Population decline
589 assessment, historical baselines, and conservation. *Conservation Letters*, **3**, 371-378.
- 590 Cardoso, P., & Leather, S.R. (2019) Predicting a global insect apocalypse. *Insect*
591 *Conservation and Diversity*, **12**, 263–267.
- 592 Cardoso, P., Branco, V.V., Chichorro, F., Fukushima, C.S., & Macías-Hernández, N. (2019)
593 Can we really predict a catastrophic worldwide decline of entomofauna and its drivers?
594 *Global Ecology and Conservation*, **20**, e00621 (doi.org/10.1016/j.gecco.2019.e00621)
- 595 Ceccaroni, L., Bibby, J., Roger, E., Flemons, P., Michael, K., Fagan, L. & Oliver, J.L. (2019).
596 Opportunities and risks for citizen science in the age of artificial intelligence. *Citizen*
597 *Science: Theory and Practice*, **4(1)**: 29, 1-14. DOI: <https://doi.org/10.5334/cstp.241>
- 598 Chaput-Bardy, A., Grégoire, A., Baguette, M., Pagano, A., & Secondi, J. (2010). Condition
599 and phenotype-dependent dispersal in a damselfly, *Calopteryx splendens*. *PloS One*, **5(5)**,
600 e10694. doi:10.1371/journal.pone.0010694.

- 601 Cohen, J.M., Lajeunesse, M.J. & Rohr, J.R. (2018) A global synthesis of animal phenological
602 responses to climate change. *Nature Climate Change*, **8**, 224-228.
- 603 Collins, C.M., Vaskou, P. & Kountouris, Y. (2019) Insect food products in the western world:
604 assessing the potential of a new “green” market. *Annals of the Entomological Society of*
605 *America*, (Special Collection: Insects as Food and Feed), pp. 1–11. doi:
606 10.1093/aesa/saz015.
- 607 Corlett, R.T. (2016) Restoration, reintroduction, and rewilding in a changing world. *Trends in*
608 *Ecology & Evolution*, **31**, 453-462.
- 609 Dallas, T.A., Saastamoinen, M., Schulz, T. & Ovaskainen, O. (2020) The relative importance
610 of local and regional processes to metapopulation dynamics. *Journal of Animal Ecology*,
611 <https://doi.org/10.1111/1365-2656.13141>
- 612 Dee, L.E., Cowles, J., Isbell, F., Pau, S., Gaines, S.D. & Reich, P.B. (2019) When do
613 ecosystem services depend on rare species? *Trends in Ecology & Evolution*, **34**, 746-758.
- 614 Denno, R.F. & Peterson, M.A. (1995) Density-dependent dispersal and its consequences for
615 population dynamics. Pages 113-130 in Cappuccino, N. & Price, P.W. (eds) *Population*
616 *Dynamics: New Approaches and Synthesis*. Academic Press, New York.
- 617 Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J. & Collen, B. (2014)
618 Defaunation in the Anthropocene. *Science*, **345**, 401–406.
- 619 Drake, V.A. & Reynolds, D.R. (2012) *Radar entomology: Observing insect flight and*
620 *migration*. CABI.
- 621 Enfjäll, K. & Leimar, O. (2005). Density-dependent dispersal in the Glanville fritillary,
622 *Melitaea cinxia*. *Oikos*, **108**, 465-472.
- 623 Falk, S., Foster, G., Comont, R., Conroy, J., Bostock, H., Salisbury, A., Kilbey, D., Bennett,
624 J. & Smith, B. (2019) Evaluating the ability of citizen scientists to identify bumblebee

- 625 (*Bombus*) species. *PLoS ONE*, **14**(6), e0218614
- 626 <https://doi.org/10.1371/journal.pone.0218614>
- 627 Forister, M.L., Pelton, E.M. & Black, S.H. (2019). Declines in insect abundance and
628 diversity: we know enough to act now. *Conservation Science and Practice*, **1**, e80
629 (doi.org/10.1111/csp2.80).
- 630 Fournier, A.M.V., White, E.R. & Heard, S.B. (2019) Site-selection bias and apparent
631 population declines in long-term studies. *Conservation Biology*, **33**, 1370–1379.
- 632 Fox, R. (2013) The decline of moths in great Britain: a review of possible causes. *Insect*
633 *Conservation & Diversity*, **6**, 5–19.
- 634 Fox, R., Harrower, C.A., Bell, J.R., Shortall, C.R., Middlebrook, I. & Wilson, R.J. (2018)
635 Insect population trends and the IUCN Red List process. *Journal of Insect Conservation*,
636 **23**, 269-278.
- 637 Gallant, A.L., Euliss, N.H. & Browning, Z. (2014) Mapping large-area landscape suitability
638 for honey bees to assess the influence of land-use change on sustainability of national
639 pollination services. *PLOS ONE*, **9**:6, e99268 DOI: 10.1371/journal.pone.0099268 .
- 640 Gardiner, T. (2007) Short-term changes (2001-2005) in glow worm *Lampyrus noctiluca* L.
641 (Coleoptera: Lampyridae) abundance in Essex. *British Journal of Entomology and Natural*
642 *History*, **20**, 1-6.
- 643 Gardiner, T. & Didham, R.K. (2020) Glowing, glowing, gone? Monitoring long term trends
644 in glow-worm numbers in south-east England. *Insect Conservation & Diversity*, **13**, xxx-
645 xxx.
- 646 Gezon, Z.J., Wyman, E.S., Ascher, J.S., Inouye, D.W. & Irwin, R.E. (2015) The effect of
647 repeated, lethal sampling on wild bee abundance and diversity. *Methods in Ecology and*
648 *Evolution*, **6**, 1044-1054.

- 649 Habel, J.C., Trusch, R., Schmitt, T., Ochse, M. & Ulrich, W. (2019) Long-term large-scale
650 decline in relative abundances of butterfly and burnet moth species across south-western
651 Germany. *Scientific Reports*, 9, 14921, <https://doi.org/10.1038/s41598-019-51424-1>
- 652 Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W.,
653 Müller, A., Sumser, H., Hörren, T., Goulson, D. & de Kroon, H. (2017) More than 75
654 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS One*
655 12, e0185809.
- 656 Hallmann, C.A., Zeegers, T., van Klink, R., Vermeulen, R., van Wielink, P., Spijkers, H., van
657 Deijk, J., van Steenis, W. & Jongejans, E. (2020). Declining abundance of beetles, moths
658 and caddisflies in the Netherlands. *Insect Conservation and Diversity*, 13, xxx-xxx.
659 <https://doi.org/10.1111/icad.12377>.
- 660 Hanski, I. (1998) Metapopulation dynamics. *Nature*, 396, 41-49.
- 661 Hart, A.G. & Sumner, S. (2020) Marketing insects: can exploiting a commercial framework
662 help promote undervalued insect species? *Insect Conservation and Diversity*, 13, xxx-xxx.
- 663 Harvey, J.A., Heinen, R., Armbrrecht, I. *et al.* (2020) International scientists formulate a
664 roadmap for insect conservation and recovery. *Nature Ecology & Evolution*
665 <https://doi.org/10.1038/s41559-019-1079-8>
- 666 Hicks, B.J., Leather, S.R. & Watt, A.D. (2008) Changing dynamics of the pine beauty moth
667 (*Panolis flammea*) in Britain: the loss of enemy free space? *Agricultural & Forest*
668 *Entomology*, 10, 263-271.
- 669 Hill, J.K., Thomas, C.D., Fox, R., Telfer, M.G., Willis, S.G., Asher, J. & Huntley, B. (2012)
670 Responses of butterflies to twentieth century climate warming: implications for future
671 ranges. *Proceedings of the Royal Society of London, Series B*, 269, 2163-2171.

- 672 Hill, M.P., Gallardo, B. & Terblanche, J.S. (2017) A global assessment of climatic niche
673 shifts and human influence in insect invasions. *Global Ecology and Biogeography*, **26**,
674 679-689.
- 675 Holzschuh, A., Dormann, C.F., Tschardtke, T. & Steffan-Dewenter, I. (2011) Expansion of
676 mass-flowering crops leads to transient pollinator dilution and reduced wild plant
677 pollination. *Proceedings of the Royal Society of London, Series B*, **278**, 3444-3451.
- 678 Howard, L.C., Wood, P.J., Greenwood, M.T. & Rendell, H.M. (2009) Reconstructing
679 riverine paleo-flow regimes using subfossil insects (Coleoptera and Trichoptera): the
680 application of the LIFE methodology to paleochannel sediments. *Journal of*
681 *Paleolimnology*, **42**, 453-466.
- 682 Hu, G., Lim, K.S., Horvitz, N., Clark, S.J., Reynolds, D.R., Sapir, N. & Chapman, J.W.
683 (2016) Mass seasonal bioflows of high-flying insect migrants. *Science*, **354**, 1584-1587.
- 684 Humphries, G.R.W., Che-Castaldo, C., Bull, P.J., Lipstein, G., Ravia, A., de Carrión, B.,
685 Bolton, T., Ganguly, A. & Lynch, H.J. (2018) Predicting the future is hard and other
686 lessons from a population time series data science competition. *Ecological Informatics*,
687 **48**, 1-11.
- 688 Hüpopp, O., Ciach, M., Diehl, R., Reynolds, D.R., Stepanian, P.M. & Menz, M.H.M. (2019)
689 Perspectives and challenges for the use of radar in biological conservation. *Ecography*, **42**,
690 912-930.
- 691 Isaac, N.J.B. & Pocock, M.J.O. (2015) Bias and information in biological records. *Biological*
692 *Journal of the Linnean Society*, **115**, 522-531.
- 693 Jeliaskov, A., Bas, Y., Kerbiriou, C., Julien, J.-F., Penone, C. & Le Viol, I. (2016) Large-
694 scale semi-automated acoustic monitoring allows to detect temporal decline of bush-
695 crickets. *Global Ecology and Conservation*, **6**, 208-218.

- 696 Karlsson, D., Hartop, E., Forshage, M., Jaschhof, M. & Ronquist, F. (2020) The Swedish
697 Malaise trap project: a 15 year retrospective on a countrywide insect inventory.
698 *Biodiversity Data Journal* **8**: e47255. <https://doi.org/10.3897/BDJ.8.e47255>
- 699 Kent, C.F., Dey, A., Patel, H., Tsvetkov, N., Tiwari, T., MacPhail, V.J., Gobeil, Y., Harpur,
700 B.A., Gurtowski, J., Schatz, M.C., Colla, S.R. & Zayed, A. (2018) Conservation genomics
701 of the declining North American bumblebee *Bombus terricola* reveals inbreeding and
702 selection on immune genes. *Frontiers in Genetics*, **9**: 316.
703 <https://doi.org/10.3389/fgene.2018.00316>
- 704 Kirkeby, C., Wellenreuther, M. & Brydegaard, M. (2016) Observations of movement
705 dynamics of flying insects using high resolution lidar. *Scientific Reports* **6**, 29083.
706 <https://doi.org/10.1038/srep29083>
- 707 Komonen, A., Halme, P. & Kotiaho, J.S. (2019). Alarmist by bad design: strongly
708 popularized unsubstantiated claims undermine credibility of conservation science.
709 *Rethinking Ecology*, **4**, 17–19.
- 710 Kremen, C., Ullman, K.S. & Thorp, R.W. (2011) Evaluating the quality of citizen-scientist
711 data on pollinator communities. *Conservation Biology*, **25**: 607-617.
- 712 Langor, D.W. (2019) The diversity of terrestrial arthropods in Canada. In: Langor D.W. and
713 Sheffield, C.S. (Eds) *The Biota of Canada – A Biodiversity Assessment. Part 1: The*
714 *Terrestrial Arthropods. ZooKeys*, **819**, 9-40. <https://doi.org/10.3897/zookeys.819.31947>
- 715 Lebuhn, G., Droege, S., Connor, E.F., Gemmill-Herren, B., Potts, S.G., Minckley, R.L.,
716 Griswold, T., Jean, R., Kula, E., Roubik, D.W., Cane, J., Wright, K.W., Frankie, G. &
717 Parker, F. (2013) Detecting insect pollinator declines on regional and global scales.
718 *Conservation Biology*, **27**, 113-120.
- 719 Leibrich, J. (2006) *Nesta and the Missing Zero*. Scholastic NZ Ltd (ISBN: 1-86943-730-6).

- 720 Lister, B.C. & Garcia, A. (2018) Climate-driven declines in arthropod abundance restructure
721 a rainforest food web. *Proceedings of the National Academy of Sciences USA*, **115**,
722 E10397–E10406.
- 723 Lockwood, J.A. (2010) The fate of the Rocky Mountain locust, *Melanoplus spretus* Walsh:
724 implications for conservation biology. *Terrestrial Arthropod Reviews* **3**, 129-160.
- 725 Macgregor, C.J., Williams, J.H., Bell, J.R. & Thomas, C.D. (2019) Moth biomass increases
726 and decreases over 50 years in Britain. *Nature Ecology and Evolution*, **3**, 1645-1649.
- 727 MacPhail, V.J., Richardson, L.L. & Colla, S.R. (2019) Incorporating citizen science, museum
728 specimens, and field work into the assessment of extinction risk of the American Bumble
729 bee (*Bombus pensylvanicus* De Geer 1773) in Canada. *Journal of Insect Conservation*, **23**,
730 597-611.
- 731 Martin, B.T., Munch, S.B. & Hein, A.M. (2018) Reverse-engineering ecological theory from
732 data. *Proceedings of the Royal Society of London, Series B*, **285**, 20180422.
733 <http://dx.doi.org/10.1098/rspb.2018.0422>
- 734 McGeachie, W.J. (1989) The effects of moonlight illuminance, temperature and wind speed
735 on light-trap catches of moths. *Bulletin of Entomological Research* **79**, 185-192.
- 736 Minnaar, C., Boyles, J.G., Minnaar, I.A., Sole, C.L. & McKechnie, A.E. (2015) Stacking the
737 odds: light pollution may shift the balance in an ancient predator-prey arms race. *Journal*
738 *of Applied Ecology* **52**, 522-531.
- 739 Møller, A.P. (2019) Parallel declines in abundance of insects and insectivorous birds in
740 Denmark over 22 years. *Ecology and Evolution*, **9**, 6581– 6587.
741 <https://doi.org/10.1002/ece3.5236>
- 742 Montgomery, G.A., Dunn, R.R., Fox, R., Jongejans, E., Leather, S.R., Saunders, M.E.,
743 Shortall, C.R., Tingley, M.W. & Wagner, D.L. (2020) Is the insect apocalypse upon us?
744 How to find out. *Biological Conservation*, doi.org/10.1016/j.biocon.2019.108327.

- 745 Mupepele, A.C., Bruelheide, H., Dauber, J., Krüß, A., Potthast, T., Wägele, W. & Klein,
746 A.M. (2019) Insect decline and their drivers: unsupported conclusions in a poorly
747 performed meta-analysis on trends—a critique of Sánchez-Bayo and Wyckhuys (2019).
748 *Basic and Applied Ecology*, **37**, 20–23.
- 749 Noskova, E., Ulyantsev, V., Koepfli, K.P., O'Brien, S.J. & Dobrynin, P. (2019) GADMA:
750 Genetic algorithm for inferring demographic history of multiple populations from allele
751 frequency spectrum data. *BioRxiv*. 2019 Jan 1:407734.
- 752 Oliver, T.H., Powney, G.D., Baguette, M. & Schtickzelle, N. (2017). Synchrony in
753 population counts predicts butterfly movement frequencies. *Ecological Entomology*, **42**,
754 375-378.
- 755 Outhwaite, C.L., Chandler, R.E., Powney, G.D., Collen, B., Gregory, R.D. & Isaac, N.J.B.
756 (2018). Prior specification in Bayesian occupancy modelling improves analysis of species
757 occurrence data. *Ecological Indicators*, **93**, 333-343.
- 758 Ovaskainen, O. & Saastamoinen, M. (2018) Frontiers in metapopulation biology: the legacy
759 of Ilkka Hanski. *Annual Review of Ecology, Evolution and Systematics*, **49**, 231-252.
- 760 Owens, A.C.S., Cochard, P., Durrant, J., Farnworth, B., Perkin, E.K. & Seymoure, B. (2020)
761 Light pollution is a driver of insect declines. *Biological Conservation*
762 (<https://doi.org/10.1016/j.biocon.2019.108259>)
- 763 Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts
764 across natural systems. *Nature*, **421**, 37-42.
- 765 Pilotto, F., Nilsson, C., Polvi, L.E. & McKie, B.G. (2018) First signs of macroinvertebrate
766 recovery following enhanced restoration of boreal streams used for timber floating.
767 *Ecological Applications*, **28**, 587-597.
- 768 Pollard, E. (1991) Synchrony of population fluctuations - the dominant influence of
769 widespread factors on local butterfly populations. *Oikos*, **60**, 7-10.

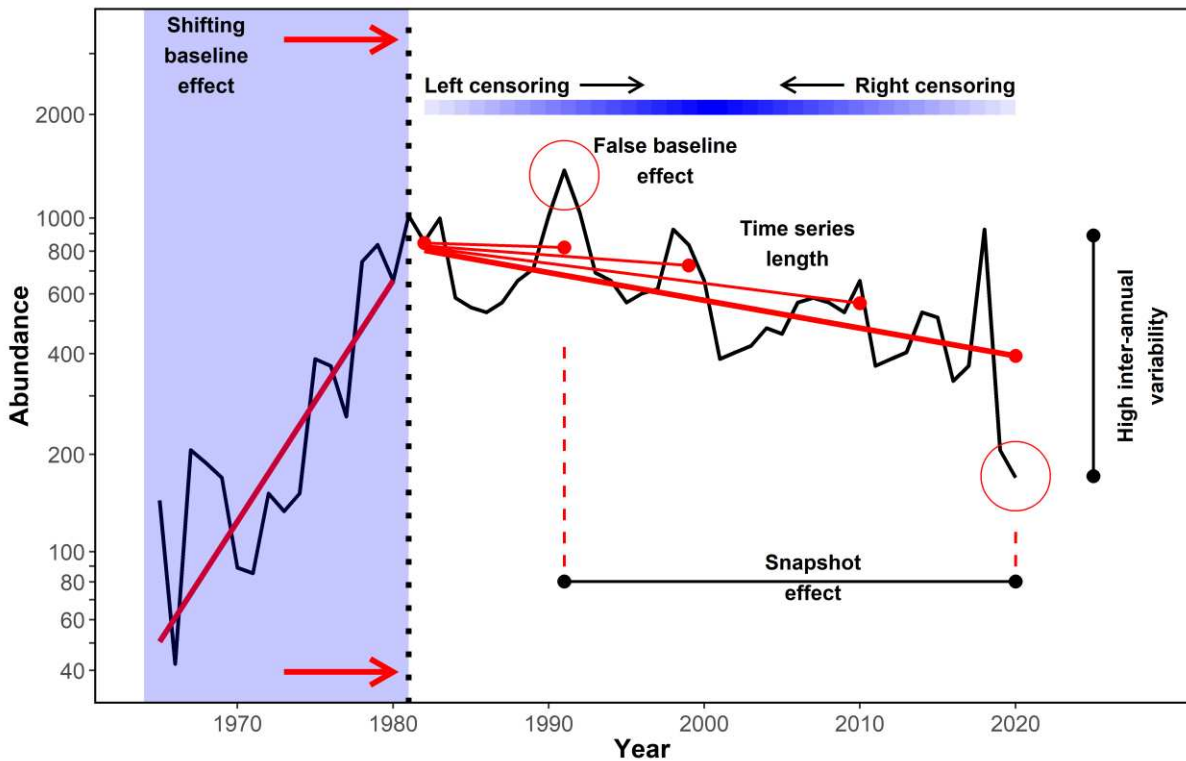
- 770 Powney, G.D., Carvell, C., Edwards, M., Morris, R.K.A., Roy, H.E., Woodcock, B.A. &
771 Isaac, N.J.B. (2019) Widespread losses of pollinating insects in Britain. *Nature*
772 *Communications*, **10**, 1018 (doi.org/10.1038/s41467-019-08974-9).
- 773 Ruczyński, I., Hałat, Z., Zegarek., M., Borowik, T. & Dechmann, D.K.N. (2020) Camera
774 transects as a method to monitor high temporal and spatial ephemerality of flying
775 nocturnal insects. *Methods in Ecology and Evolution*, [https://doi.org/10.1111/2041-](https://doi.org/10.1111/2041-210X.13339)
776 [210X.13339](https://doi.org/10.1111/2041-210X.13339)
- 777 Rabl, D., Rabl, C. & Rabl, S. (2017) The Mediterranean distributed Cypress jewel beetle
778 *Ovalisia festiva* (Linnaeus, 1767) has reached the east of Austria (Coleoptera:
779 Buprestidae). *Entomologische Zeitschrift*, **127**, 109-111.
- 780 Redfearn, A. & Pimm, S.L. (1988) Population variability and polyphagy in herbivorous
781 insect communities. *Ecological Monographs*, **58**, 39-55
- 782 Régnière, J. & Nealis, V.G. (2019) Density dependence of egg recruitment and moth
783 dispersal in spruce budworms. *Forests*, **10**, 706 (doi.org/10.3390/f10080706).
- 784 Roquette, J.R. & Thompson, D.J. (2007) Patterns of movement and dispersal in an
785 endangered damselfly and the consequences for its management. *Journal of Applied*
786 *Ecology*, **44**, 692-701.
- 787 Roubik, D.W. (2001) Ups and downs in pollinator populations: When is there a decline?
788 *Conservation Ecology*, **5(1):2**. [online] URL: <http://www.consecol.org/vol5/iss1/art2/>
- 789 Sánchez-Bayo, F. & Wyckhuys, K.A.G. (2019) Worldwide decline of the entomofauna: a
790 review of its drivers. *Biological Conservation*, **232**, 8–27.
- 791 Saunders, M.E., Janes, J.K. & O’Hanlon, J.C. (2020a) Moving on from the insect apocalypse
792 narrative: engaging with evidence-based insect conservation. *BioScience*, **70**, 80-89.

- 793 Saunders, M.E., Janes, J. & O’Hanlon, J. (2020b) Semantics of the insect decline narrative:
794 recommendations for communicating insect conservation to peer and public audiences.
795 *Insect Conservation and Diversity*, **13**, **ICDIV-20-0035**.
- 796 Saunders, S.P., Farr, M.T., Wright, A.D., Bahlai, C.A., Ribeiro, J.W., Rossman, S., Sussman,
797 A.L., Arnold, T.W. & Zipkin, E.F. (2019) Disentangling data discrepancies with
798 integrated population models. *Ecology* **100(6)**:e02714. <https://doi.org/10.1002/ecy.2714>.
- 799 Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarli, D., Ammer, C.,
800 Bauhus, J., Fischer, M., Habel, J.C., Linsenmair, K.E., Nauss, T., Penone, C., Prati, D.,
801 Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S. & Weisser, W.W. (2019) Arthropod
802 decline in grasslands and forests is associated with landscape-level drivers. *Nature*, **574**,
803 671-674.
- 804 Simmons, B.I., Balmford, A., Bladon, A.J., Christie, A.P., De Palma, A., Dicks, L.V.,
805 Gallego-Zamorano, J., Johnston, A., Martin, P.A., Purvis, A., Rocha, R., Wauchope, H.S.,
806 Wordley, C.F.R., Worthington, T.A. & Finch, T. (2019) Worldwide insect declines: an
807 important message, but interpret with caution. *Ecology and Evolution*, **9**, 3678–3680.
- 808 Shortall C.R., Moore A., Smith E., Hall M.J., Woiwod I.P. & Harrington R. (2009) Long-
809 term changes in the abundance of flying insects. *Insect Conservation and Diversity*, **2**,
810 251–260.
- 811 Soga, M. & Gaston, K.J. (2018). Shifting baseline syndrome: causes, consequences, and
812 implications. *Frontiers in Ecology and Environment*, **16**, 222–230.
- 813 Speight, M.C.D. (1989). *Saproxyllic Invertebrates and Their Conservation*. Nature and
814 Environment Series, vol. 42, pages 1-79. Council of Europe, Strasbourg.
- 815 Stepanian, P.M., Entrekin, S.A., Wainwright, C.E., Mirkovic, D., Tank, J.L. & Kelly, J.F.
816 (2020) Declines in an abundant aquatic insect, the burrowing mayfly, across major North

- 817 American waterways. *Proceedings of the National Academy of Sciences USA*, 201913598;
818 DOI: 10.1073/pnas.1913598117
- 819 Stribling, J.B., Pavlik, K.L., Holdsworth, S.M. & Leppo, E.W. (2008). Data quality,
820 performance, and uncertainty in taxonomic identification for biological
821 assessments. *Journal of the North American Benthological Society*, **27**, 906-919.
- 822 Sutcliffe, O.L., Thomas, C.D. & Moss, D. (1996) Spatial synchrony and asynchrony in
823 butterfly population dynamics. *Journal of Animal Ecology* **65**, 85-95.
- 824 Thomas, C.D., Jones, T.H. & Hartley, S.E. (2019) “Insectageddon”: a call for more robust
825 data and rigorous analyses. *Global Change Biology*, **25**, 1891-1892.
- 826 Thomson J.D. (2010). Flowering phenology, fruiting success, and progressive deterioration
827 of pollination in an early-flowering geophyte. *Philosophical Transactions of the Royal
828 Society of London. Series B: Biological Sciences*, **365**, 3187–3199.
- 829 Thomson, J.D. (2019) Progressive deterioration of pollination service detected in a 17-year
830 study vanishes in a 26-year study. *New Phytologist*, **224**, 1151-1159.
- 831 van der Wal, R., Sharma, N., Mellish, C., Robinson, A. & Siddharthan, A. (2016) The role of
832 automated feedback in training and retaining biological recorders for citizen science.
833 *Conservation Biology*, **30**, 550–61.
- 834 van Huis, A. (2017) Edible insects: marketing the impossible? *Journal of Insects as Food and
835 Feed*, **3**, 67-68. doi: 10.3920/JIFF2017.x003.
- 836 Vogel, G. (2017) Where have all the insects gone? *Science*, **356**, 576-579.
- 837 Wagner, D.L. (2019) Global insect decline: comments on Sánchez-Bayo and Wyckhuys
838 (2019). *Biological Conservation*, **233**, 334–335.
- 839 Wagner, D.L. (2020). Insect declines in the Anthropocene. *Annual Review of Entomology*,
840 **65**, 457-480.

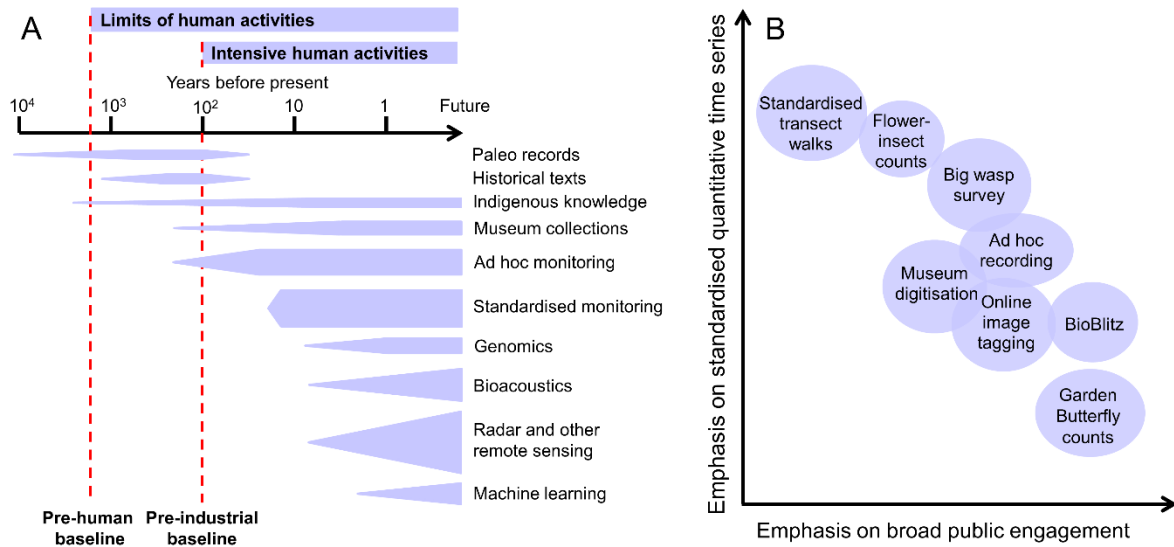
- 841 Wäldchen, J. & Mäder, P. (2018) Machine learning for image based species identification.
842 *Methods in Ecology and Evolution*, **9**, 2216-2225.
- 843 Walther, G.-R., Roques, A., Hulme, P.E., Sykes, M.T., Pyšek, P., Kühn, I., Zobel, M.,
844 Bacher, S., Botta-Dukát, Z., Bugmann, H., Czúcz, B., Dauber, J., Hickler, T., Jarošík, V.,
845 Kenis, M., Klotz, S., Minchin, D., Moora, M., Nentwig, W., Ott, J., Panov, V.E.,
846 Reineking, B., Robinet, C., Semenchenko, V., Solarz, W., Thuiller, W., Vilà, M., Vohland,
847 K. & Settele, J. (2009) Alien species in a warmer world: risks and opportunities. *Trends in*
848 *Ecology & Evolution*, **24**, 686-693.
- 849 Ward, D.F., New, T.R. & Yen, A.L. (2001) Effects of pitfall trapping on the abundance,
850 richness and composition of invertebrate catches. *Journal of Insect Conservation*, **5**, 47-
851 53.
- 852 Watt, A.D. & Hicks, B.J. (2000) A reappraisal of the population dynamics of the pine beauty
853 moth, *Panolis flammea*, on lodgepole pine, *Pinus contorta*, in Scotland. *Population*
854 *Ecology*, **42**, 225-230.
- 855 Wepprich, T., Adrion, J.R., Ries, L., Wiedmann, J. & Haddad, N.M. (2019) Butterfly
856 abundance declines over 20 years of systematic monitoring in Ohio, USA. *PLoS One*, **14**,
857 e0216270.
- 858 Westphal, C., Bommarco, C., Carré, G., Lamborn, E., Morison, N., Petanidou, T., Potts, S.G.,
859 Roberts, S.P.M., Szentgyörgyi, H., Tscheulin, T., Vaissière, B.E., Woyciechowski, M.,
860 Biesmeijer, J.C., Kunin, W.E., Settele J. & Steffan-Dewenter, I. (2008) Measuring bee
861 diversity in different European habitats and biogeographical regions. *Ecological*
862 *Monographs*, **78**, 653-671.
- 863 White, E.R. (2019). Minimum time required to detect population trends: the need for
864 longterm monitoring programs. *BioScience*, **69**, 40–46.

- 865 Wilf, P., Labandeira, C.C., Johnson, K.R., Coley, P.D. & Cutter, A.D. (2001) Insect
866 herbivory, plant defense, and early Cenozoic climate change. *Proceedings of the National*
867 *Academy of Sciences USA*, **98**, 6221-6226.
- 868 Willig, M.R., Woolbright, L., Presley, S.J., Schowalter, T.D., Waide, R.B., Heartsill Scalley,
869 T., Zimmerman, J.K., González, G. & Lugo, A.E. (2019) Populations are not declining
870 and food webs are not collapsing at the Luquillo Experimental Forest. *Proceedings of the*
871 *National Academy of Sciences USA*, **116**, 12143–12144.
- 872 Winfree, R., Fox, J.W., Williams, N.M., Reilly, J.R., & Cariveau, D.P. (2015). Abundance of
873 common species, not species richness, drives delivery of a real-world ecosystem service.
874 *Ecology Letters*, **18**, 626-635.
- 875 Wotton, K.R., Gao, B., Menz, M.H.M., Morris, R.K.A., Ball, S.G., Lim, K-S., Reynolds,
876 D.R., Hu, G. & Chapman, J.W. (2019) Mass seasonal migrations of hoverflies provide
877 extensive pollination and crop protection services. *Current Biology*, **29**, 2167-2173.
878



879

880 **Figure 1.** Schematic representation of some of the potential pitfalls in quantitative estimation
 881 of population change through time. The trend line is a hypothetical (not empirical) time series
 882 of insect abundance values over 55 years, loosely based on the form of the trend line for moth
 883 biomass change in the UK in Macgregor *et al.* (2019). Without good knowledge of historical
 884 conditions, perception of changes through time can be strongly biased by shifting baseline
 885 effects. Moreover, any non-random bias toward an above-average starting point in a time
 886 series comparison could lead to a false baseline effect. This might be particularly problematic
 887 in simple pairwise snapshot effects if there is also bias in the selection of the contemporary
 888 time-point for comparison. These kinds of effects are likely to be most severe when inter-
 889 variability in abundance is high. Longer time series will increase the signal to noise ratio and
 890 statistical power. Cross-validation approaches, such as left-censoring and/or right-censoring
 891 time series, have been suggested to test the sensitivity of trends to underlying bias in the data.
 892



893

894 **Figure 2.** The range of complementary datasets that feed into entomological monitoring
 895 initiatives. (A) Datasets tend not to cover the most important period of monitoring: the time
 896 before substantial human impact. Attempts to integrate across these data sources have been
 897 minimal but are essential to understand older patterns and establish baselines. (B) The goals
 898 of citizen science monitoring programs vary on a continuum ranging from high emphasis on
 899 broad public engagement and education (e.g., for species that are easily identified, such as
 900 butterflies in backyard garden counts, or where substantial expert assistance can be delivered
 901 at specific times, such as in a BioBlitz), through to a higher emphasis on the collection of
 902 standardised quantitative time series data (e.g., for recording changes in regional occupancy
 903 patterns through time, or standardised transect walks for temporal trends in abundance)
 904 potentially requiring a greater investment in training of citizen scientists and data validation
 905 by experts.