# 1 Using causal diagrams and superpopulation models

2 to correct geographic biases in biodiversity

# 3 monitoring data

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- 10 **Running headline:** Correcting sampling bias in biodiversity data

### 11 Abstract

- 12 1. Biodiversity monitoring schemes periodically measure species' abundances and distributions 13 at a sample of sites to understand how they have changed over time. Often, the aim is to infer 14 change in an average sense across some wider landscape. Inference to the wider landscape is 15 simple if the species' abundances and distributions are similar at sampled to non-sampled 16 locations. Otherwise, the data are geographically biased, and some form of correction is 17 desirable.
- 2. We combine causal diagrams with "superpopulation models" to correct time-varying 18 geographic biases in biodiversity monitoring data. For a given time-period, expert-derived 19 20 causal diagrams are used to deduce the set of variables that explain the geographic bias, and 21 superpopulation models adjust for these variables to produce a corrected estimate of a 22 landscape-wide mean of e.g. abundance or occupancy. Estimating a time trend in the variable 23 of interest is achieved by fitting models for multiple time-periods and, if the drivers of bias 24 are suspect to change over time, by constructing per period causal diagrams. We test the 25 approach using simulated data then apply it to real data from the UK Butterfly Monitoring 26 Scheme (UKBMS).
- 3. Where the variables that explain the geographic bias are known and measured without error, our method is unbiased. Introducing measurement error reduces the method's efficacy, but it is still an improvement on using the sample mean. When applied to data from the UKBMS, the approach gives different results to the scheme's current method, which assumes no geographic bias.
- 32 4. Where the goal is to estimate change in some variable of interest at the landscape level (e.g. 33 biodiversity indicators), models that do not adjust for geographic bias implicitly assume it 34 does not exist. Our approach makes the weaker assumption that there is no geographic bias 35 conditional on the adjustment variables, so it should yield more accurate estimates of time 36 trends in many circumstances. The method does require assumptions about the drivers of bias, 37 but these are codified explicitly in the causal diagrams. Operationalising our approach should 38 be less costly than full probability sampling, which would be needed to satisfy the 39 assumptions of conventional approaches.

Key words: Directed Acyclic Graph; expert consultation; imputation; sampling bias; species
 abundance; time trend

#### Introduction 42

#### Monitoring biodiversity 43

- 44 The goal of biodiversity monitoring is to understand how some variable of interest Y, often when
- 45 summarised across the relevant landscape or study area, has changed over time (cf. Yoccoz et al.,
- 46 2001). Y might be a species' (relative) abundance, occupancy or some summary thereof across many
- 47 species. The landscape is often delimited by national boundaries (Moussy et al., 2022), but in
- 48 principle it could be any geographic area. Y is usually summarised across the landscape periodically
- 49 by taking its mean or something similar (e.g. a categorical year effect from a model in which Y is the
- 50 response; Brereton, Roy, et al., 2011; Powney et al., 2019; Stroh et al., 2023).
- 51 To calculate the landscape-wide mean of Y directly, one would need to know its distribution across
- 52 the landscape as a whole (i.e. its value at every location). Generally, however, the landscape
- 53 distribution of Y is not known, because it is not possible to collect data at every location. Instead, the
- 54 usual strategy is to split the landscape into areal units, or "sites", and to collect data at some of them.
- 55 The landscape-wide mean of Y is then *estimated* from the sample of sites for which data are available.
- 56 Geographic sampling biases
- When estimating the landscape-wide mean of *Y* from a sample of sites, there is a risk of geographic 57
- 58 sampling bias. A dataset is geographically biased if the distribution of Y across sampled sites differs
- 59 from its distribution across the wider landscape. An equivalent definition is the existence of a non-
- zero correlation between Y and a sample inclusion indicator R, which takes the value 1 at sampled 60
- sites and 0 elsewhere (Boyd, Powney, et al., 2023; Meng, 2018). If the correlation is positive, then the 61
- 62 bias is positive (i.e. the mean of Y is larger across sampled sites than across the landscape as a whole),
- 63 and vice versa. The greater the magnitude of the correlation, the more severe the bias.
- 64 Biodiversity monitoring data are often collected in such a way that the same factors affect R and Y.
- 65 which induces a correlation between the two (and therefore a bias). To give one simple example
- (many others are possible), Y might be some species' abundance, which is positively affected by 66
- 67 habitat quality. Habitat quality might also have a positive effect on R, because data collectors are
- 68 often volunteer naturalists (i.e. citizen scientists) and prefer to visit sites that are interesting in terms
- of wildlife (Bowler et al., 2022; Forister et al., 2023). In this situation, Y would be larger at sampled 69 70 sites, which is to say that there would be a positive bias. The reverse would be true if sampling was
- 71 more likely at sites where species are faring poorly: say, in built-up areas that have poor quality
- 72 habitat, but which are easy for recorders to access by road (Hughes et al., 2020).
- 73 Data from structured monitoring schemes are less susceptible to geographic biases than those from
- 74 most other sources (Geldmann et al., 2016), but they are not immune. Many structured monitoring
- 75 schemes aim to collect data at a random sample of sites (e.g. Pescott et al., 2019; Robbins et al.,
- 1986). If implemented properly, random sampling ensures no correlation between R and Y in 76
- 77 expectation (i.e. on average over many possible samples; see Meng, 2018). Obtaining a true random
- 78 sample is challenging, however, especially if there is a reliance on volunteers to collect the data
- 79 (which is true of many monitoring schemes). The volunteers might be unwilling or unable to visit 80 some randomly selected sites, whether because they are difficult to access, uninteresting in terms of
- 81 wildlife or for some other reason (Pescott et al., 2015). Nominally random samples with incomplete
- 82 uptake of sites, or "nonresponse" in survey sampling parlance, are almost certain to be biased (Bailey,
- 83 2023).

#### 84 Mitigating geographic biases

- Various approaches exist to mitigate sampling biases, most of which exploit the fact that some set of 85
- 86 variables A could explain the correlation between R and Y (Lohr, 2022; Meng, 2022). If, to use the
- 87 above example, R and Y are both greater at sites with good quality habitat, then the presence of that
- habitat will explain some of the correlation between the two. Where the variables in A can be 88
- 89 identified—a point we come back to below—and are reflected in available data, statistically
- 90 "adjusting for" them will reduce the sampling bias (Collins et al., 2001; Mohan et al., 2013).

- 91 One way to adjust for A is to fit a "superpopulation model", which is a regression (or other type of)
- 92 model for *Y* that includes *A* as covariates (Elliott & Valliant, 2017). In effect, the superpopulation
- 93 model stratifies sites based on levels of *A* and predicts the average or expected value of *Y* for each
- 94 stratum. If A explains the correlation between R and Y, the two should be uncorrelated within each
- 95 stratum, and the predicted within-stratum means should be close to their true values (as there is no 96 sampling bias). Averaging the within-stratum means of Y with respect to the distribution of A across
- sampling bias). Averaging the within-stratum means of Y with respect to the distribution of A across
  all sites in the landscape yields an "adjusted" estimate of the landscape-wide mean of Y (i.e. the target
- 97 an sites in the landscape yields an adjusted estimate of the landscape-wide mean of *F* (i.e. the targe 98 quantity). More simply, the average of the superpopulation predictions across all sites is the estimate
- 99 of the landscape-wide mean—or, in practice, the average of the predictions for non-sampled sites and
- 100 the observations for sampled sites (Elliott & Valliant, 2017)—and it is unbiased if A completely
- 101 explains the geographic bias.
- 102 Causal diagrams and what to adjust for
- 103 To identify the variables in A, insight can be gleaned from causal inference, where a similar challenge
- arises. Recall that *A* is the set of variables that explains the correlation between *R* and *Y*. In causal
- 105 inference, where to goal is to estimate the causal effect of one variable on another, analysts must
- 106 identify and adjust for the set of variables that explain the non-causal portion of the correlation
- 107 between the two (Pearl et al., 2016). One way to identify these variables, which could also be used to
- 108 identify the variables in *A*, is to construct "causal diagrams"(Greenland et al., 1999; Thoemmes &
- 109 Mohan, 2015).
- 110 Causal diagrams—not to be confused with parametric structural equation models—will not be

familiar to some ecologists (but see Grace & Irvine, 2020), so we will introduce the relevant concepts

- using the example in Fig 1 (a full description of the graph in Fig. 1 is provided in the Methods
- section). An arrow from one variable to another indicates a direct causal effect; that is, it indicates that
- the cause is part of the real-world function that determines the value of the effect (Pearl et al., 2016).
- In Fig. 1, annual temperature (annual\_temp) has a direct effect on *Y*, which is a species' abundance. A
- path consists of several variables linked by arrows regardless of the direction of those arrows. Fig. 1
- depicts a path linking R (site inclusion) to Y:  $R \leftarrow$  heather\_grass  $\rightarrow$  heather\_grass\_quality  $\rightarrow$  Y. The
- existence of a path between two variables implies that they are correlated, whether by association or a
- 119 causal link. Hence, Fig. 1 implies a correlation between *R* and *Y* and therefore a geographic bias.



### 120

- Figure 1. A simplistic causal diagram depicting causes and effects of sample inclusion *R* and a species' abundance *Y*.
- 123 While a path between two variables implies that they are correlated (dependent), it does not imply that
- 124 the dependence is unbreakable. Rather, it might be possible to "block" paths between variables, which
- is to say, to block the flow of association. Blocking a path is achieved by adjusting for certain
- 126 variables (i.e. *A*), and a set of rules—the rules of d-separation—tell us which ones (Cinelli et al.,

- 127 2022; Pearl et al., 2016). It is not necessary to spell out the rules of d-separation here, partly because
- they are described elsewhere (see the references above) and partly because they are built into software
- packages such as the R package dagitty (Textor et al., 2016). The important point is that the rules
- 130 can be used to determine the sets of variables A that, when statistically adjusted for, will render R and
- 131 *Y* independent (if such a set exists; Thoemmes & Mohan, 2015).
- 132 Identifying the correct set of variables in A is contingent on the causal diagram being an accurate
- reflection of reality, and there are broadly two ways to achieve this (which are not mutually
- 134 exclusive). One is to consult domain experts, who understand the relevant system, when constructing
- the diagram (Grace & Irvine, 2020). The other is to develop the diagram iteratively and test the
- implied conditional independencies (according to the rules of d-separation) of each iteration (Pearl et
- al., 2016). Where data are missing on Y for most sites (i.e. where R = 0), it will not be possible to test
- 138 many of a diagram's implied conditional independencies, in which case consulting domain experts is 139 even more important than usual. Of course, experts cannot be expected to have a perfect
- 140 understanding of most systems, and we come back to this point in several places below.
- 141 Structure of this paper
- 142 In this paper, we demonstrate how one might combine expert knowledge with causal diagrams and
- superpopulation models to mitigate geographic biases in biodiversity monitoring data. We assume that
- a time trend in the mean of Y across all sites in the relevant landscape is the target quantity, and it is
- estimated by fitting separate superpopulation models for each of several time-periods. Starting with
- some simple simulations, we test the abilities of superpopulation models including *A* as covariates to
- recover the landscape-wide mean of *Y* from perfect and imperfect (i.e. including measurement error)
  data on *A*. Next, we apply our method to empirical data from the UK Butterfly Monitoring Scheme
- (UKBMS). The scheme estimates time trends in the mean abundances butterflies in the UK using a
- 150 model that does not adjust for geographic bias, and we compare these trends to those produced using a
- 151 superpopulation models. In the final section, we discuss the pros and cons of our approach and how it
- 152 could be improved in future.

## 153 Methods

- 154 Demonstrating superpopulation modelling via simulation
- 155 Although superpopulation models can mitigate geographic biases in theory, reality is more complex.
- 156 It is likely, for example, that data will not be available on some variable(s) in A at the exact location
- 157 of a site. Instead, the available data might represent an average across some larger area in which the
- site is situated. Alternatively, data might be available on A at the precise location of the site but not
- 159 for the relevant time-period. In these cases, we would expect the data to correlate with the true
- 160 variable(s) in A, but not to be a perfect proxy. To test the implications of including imperfect data on
- 161 *A* in a superpopulation model, as well as some other methodological choices, we conducted a simple
- simulation study. (See supplementary material three for an additional simulation that includes two
- 163 time-periods and the estimation of a trend.)
- 164 Our simulation was based on the causal diagram in Fig. 1. The diagram depicts the causes of some
- 165 species' abundance Y and sample inclusion R across 250,000 sites in a simple virtual landscape. It
- 166 implies that the quantity of good quality heather grassland (heather\_grass\_quality) and annual
- 167 temperature at each site directly affect Y. The quantity of good quality heather grassland at a site is
- determined by the total quantity of heather grassland (of any quality; heather\_grass) and the
- 169 proportion that is well managed (management). *R* is greater at sites with more heather grassland,
- because recorders know that it is a favourable habitat for the focal species, which they hope to see.
- 171 The presence of major roads near a site makes it more accessible so also affect R. According to the
- rules of d-separation, the causal diagram in Fig. 1 implies that R is independent of Y given heather
- 173 grassland (i.e. there is only variable in *A*).
- 174 To simulate the data, we used the simulateSEM function in the R package dagitty (Textor et al.,
- 175 2016). With the exception of R, all variables are standard normal (i.e. mean of 0 and unit variance).
- 176 Other than causes of R (see below), each variable explains ~25% of the variation in its direct

- 177 descendent. *R* is a binary variable (0 if the data is missing and 1 otherwise), so we could not simulate
- 178 it in the same way as the others. Instead, following Thoemmes & Rose (2014), we simulated a latent
- standard normal variable and discretized it by assigning all values above the first percentile the value
- 180 1 and the remainder the value 0 (i.e. we assume data on Y are missing for 99% of sites). A
- 181 consequence of this strategy is that each cause of R explains less than 25% of its variance, because
- 182 discretizing the latent normal variable attenuates the correlation between the two. Strictly speaking,
- the latent normal variable should be included in the causal diagram in Fig 1, but it does not affect its
- 184 implied conditional independencies, so we omit it for simplicity.
- 185 Having simulated the data, we estimated the mean of *Y* across all sites using the data at sites where
- 186 R = 1 (i.e. the sample). We used six estimators, which are listed in Table 1. The first is the sample
- 187 mean, and the remainder are superpopulation models—in this case, linear regressions—including
- 188 different covariates. The first superpopulation model includes *A* (heather\_grass) as a covariate. The 189 second includes *A* and an additional cause of *Y* (annual temp), which should increase precision
- 190 (Cinelli et al., 2022). The remainder of the superpopulation models include correlates of *A* (with
- different strengths of correlation) to reflect the fact that the available data are unlikely to be error-free.
- 192 Table 1. Six analytical approaches to estimating the mean of *Y* (species abundance) across all sites in
- the simulated landscape. The adjustment set is the set of covariates included in the superpopulation
- 194 model.

Estimator	Adjustment set	Details
1	NA	Sample mean
2	heather_grass	Superpopulation model
3	heather_grass, annual_temp	Superpopulation model
4	correlate of heather_grass ( $\rho = 0.5$ )	Superpopulation model
5	correlate of heather_grass ( $\rho = 0.7$ )	Superpopulation model
6	correlate of heather_grass ( $\rho = 0.9$ )	Superpopulation model

196 We evaluated the superpopulation models' performances in terms of their estimation error. The

- 197 procedure involved simulating 100 datasets based the causal diagram in Fig. 1 and calculating the
- 198 difference between the true, landscape-wide mean of *Y* and the superpopulation model estimate for
- each one. The 100 datasets differed slightly from one another, as there is a random component to the
- simulateSEM function. Averaging the estimation error across the 100 estimates of mean *Y* for each
- 201 method gives an estimate of its estimator bias.

### 202 UKBMS case study

- 203 The scheme
- 204 To demonstrate how causal diagrams and superpopulation models might be used to correct biases in a
- real dataset, we applied them to data from the UK Butterfly Monitoring Scheme (UKBMS). The
- 206 UKBMS has been running since 1976 (Pollard & Yates, 1996). Data are collected by volunteers, who
- 207 walk transects at a network of sites in the UK and count the butterflies that they see within an
- 208 imaginary 5-metre box when weather permits (Pollard, 1977). The volunteers are free to decide where
- to establish transects and generally do so in good quality semi-natural habitat, where butterflies are
- 210 most abundant (Brereton, Roy, et al., 2011). Recorders are asked to walk UKBMS transects at least
- 211 once in each of the 26 weeks from April 1<sup>st</sup> to September 29<sup>th</sup> to cover the main flight periods of UK
- butterflies. On average, however, ~20 weeks are sampled due to poor weather conditions, recorder
- availability etc.
- In 2009, the Wider Countryside Butterfly Survey (WCBS) was established and incorporated in the
- 215 UKBMS. The primary motivation for the WCBS was to increase coverage of habitats that were
- 216 poorly represented by the UKBMS (Brereton, Cruickshanks, et al., 2011). Hence, rather than being
- 217 chosen by the volunteers, WCBS sites are located within randomly selected 1 km grid squares in the
- 218 UK. Importantly, however, volunteers are not willing/able to visit all WCBS squares: they prefer to
- visit and to re-visit sites that are accessible or where they are likely to see species that interest them.

- 220 Consequently, WCBS squares are not truly random. WCBS transects also differ from traditional
- 221 UKBMS transects in that volunteers are asked to walk them a minimum of twice in July–August
- 222 (although some do more) at least ten days apart.

#### 223 Existing analytical method

- 224 The current method used to analyse the UKBMS (including WCBS) data has three steps (Dennis et
- al., 2016). The first is to fit a GAM to estimate normalised seasonal abundance curves for each
- species and year (these do not vary geographically; Dennis et al., 2013). The second is to estimate
- annual site indices of relative abundance using the fitted GAMs. The total observed counts are scaled
- by the proportion of the seasonal abundance curve that was surveyed to provide an estimate of the
- expected total had the entire season been surveyed. Finally, a Poisson GLM with site and year effects is fitted to the annual site indices, and the estimated year effects (log10 scale) are used as annual
- indices of relative abundance. In the final GLM, each site/year index is weighted in proportion to the
- fraction of the 26-week flight curve that was sampled (rather than imputed). Consequently, the WCBS
- sites, which are sampled as little as twice per year, should be heavily downweighted.

### 234 New analytical method

- 235 We modified the current UKBMS framework by replacing the final GLM with superpopulation
- models that adjust for A. Steps one and two, which produce seasonally adjusted annual site indices of
- relative abundance, remain the same, and the superpopulation models are fitted to these indices.
- 238 Taxon and dataset experts provided the information needed to construct causal diagrams and identify
- the variables in *A* (more details below).
- 240 For demonstrative purposes, we focused on two species of butterfly, whose geographic distributions
- and ecologies are very different: the meadow brown (*Maniola jurtina*) and the small pearl-bordered
- fritillary (*Boloria selene*). The causes and effects of *Y*, i.e. relative abundance, differ between the two
- species. As we are only working with one dataset, collected by the UKBMS (including WCBS sites),
- 244 the causes and effects of R (site inclusion) do not differ between species.
- 245 We asked two taxon and UKBMS experts to provide information on the causes and effects of *R* and *Y*
- via the forms in supplementary materials one and two. Both experts (redacted) are authors on this
- 247 paper. To constrain their answers, we asked the experts to select causes and effects from a list of 49
- 248 land cover (i.e. habitat), bioclimatic, geological and other variables on which data are available (see 249 supplementary material three for details of the data). Of course, this strategy risks omitting important
- 249 supplementary material three for details of the data). Of course, this strategy fisks omitting important 250 variables—a point we come back to in the Discussion. The experts provided their feedback
- 251 independently.
- 252 Rather than the transect-level, we asked the experts to think about causes and effects of *R* and *Y* at the
- 253 coarser resolution of  $1 \times 1$  km, which was necessary for two reasons. First, it is the finest resolution
- at which data on some variables in A are available. The second reason is more complex. Recall that
- the superpopulation model predictions of *Y* must be averaged across all sites in the landscape. It
- would be conceptually challenging the split the landscape into imaginary transects, which are the
- 257 "true" sites, but splitting it into  $1 \times 1$  km grid squares is simple. In the few cases where multiple
- 258 UKBMS transects fell within the same grid square, we averaged the site indices across those transects
- in a given year to obtain a grid square-level data point.
- 260 The information provided by the experts enabled us to construct causal diagrams and, using the rules
- 261 of d-separation, to identify the variables in A (according to each expert). In total, we produced four
- 262 causal diagrams: one for each species and expert. For any one diagram, there may be multiple sets of
- 263 variables A that d-separate R and Y. We selected the "minimal" (i.e. smallest) set that only included
- variables on which data are available (listed in Table 2).
- Both experts indicated that some land cover (habitat) types have negative effects on R and Y, but we
- did not include these in the causal diagrams. Our logic is that these land cover types are only
- detrimental to the species in the sense that they are not the right habitat (indeed, this is how it was
- phrased by expert two [redacted]). The land cover data are expressed as the proportion of each 1 km arid square covered by each land cover type (Marton et al. 2022) which means that a large
- 269 grid square covered by each land cover type (Morton et al., 2022), which means that a large

- 270 proportion of one necessarily means a small proportion of another (i.e. the land cover types are not
- 271 independent). That is, a high proportion of favourable habitat would imply a low proportion of
- 272 unfavourable habitat, and vice versa, so it is not necessary to include unfavourable land cover types in
- the causal diagrams.
- Having identified two sets of variables A (one from each expert) for each species, the next step was to
- fit superpopulation models including these variables as covariates. We fitted one model per species,
- expert (i.e. *A*) and year. As the data are (normalised) counts, and for consistency with the current
   UKBMS method, we used Poisson GLMs with a log link function. We used each model to predict *Y*
- for non-sampled sites, combined the predictions with the observations at sampled sites and calculated
- the mean for the relevant species and year. Each year's mean for a given expert and species gives an
- annual index of abundance. To measure change over time, we used the slope from a regression of the
- 281 estimated abundance indices on year.
- For simplicity, we treated the model covariates (i.e. *A*) as constant over time. This was a natural
- 283 choice for elevation and calcareous bedrock, which are genuinely time-invariant (at least since 1976).
- Our approach might seem less appropriate for the three land cover classes that featured in at least one
- of the models (Table 2), but inspection of the available land cover maps shows that there has been
- 286 little change in the recent past (85% of  $25 \times 25$  m grid squares in Great Britain were the same land
- cover class in 2015 as in 1990; supplementary material three). Full details of the auxiliary data are
- 288 provided in supplementary material three.
- 289 Comparing trends from the current and new methods
- 290 Some rescaling was needed to ensure comparability between the outputs of the current UKBMS
- analysis and the superpopulation models. The year effects from the current UKBMS model represent
- the average change in the focal species' relative abundance across sites in the relevant year relative to
- a reference year (1976) on the log10 scale. The estimates from the superpopulation models, on the
- other hand, reflect the average absolute count across sites in each year on the natural log scale. To match the two, we converted the natural log estimates from the superpopulation models to the log10
- scale then subtracted the estimate from the reference year from each year's index.
- 297 Variance estimation
- 298 For both the superpopulation models and the simpler GLM used by the UKBMS, we estimated the
- sampling variance in each year's index of relative abundance by bootstrapping across sites. We
- 300 created 100 bootstrap samples by resampling the site indices with replacement within each year and
- fitted a model to each sample. We present percentile (95%) confidence intervals for each year from
- the bootstrap distribution of the annual indices (year effects from the simple GLM and estimates of
- 303 mean *Y* from the superpopulation models). Note that this procedure does not propagate uncertainty in
- the estimation of the site indices from the raw count data.

# 305 Results

## 306 Simulations

- Fig. 2 shows the estimation error—the difference between the true, landscape-wide mean of *Y* and the estimate thereof—of each analytical method listed in Table 1. The sample mean is highly biased
- 309 (mean error, i.e. bias, of ~0.35 in units of standard deviations of Y). Using a superpopulation in which
- 310 A is the sole covariate (A comprises just one variable in this example), the estimate of mean Y across
- all sites is unbiased (scenario 2; mean error~0). The estimate is also unbiased if A plus an additional
- 312 cause of *Y* are included as covariates (scenario 3), and it has similar variance to the estimate from
- 313 scenario 2. Including a correlate of A as the covariate reduces the bias relative to the sample mean but
- does not eliminate it (scenarios 4-6; see Table 1). The stronger the correlation between A and its
- 315 proxy, the closer the bias to that from scenario 2, where A itself was included as a covariate.







thereof) under each of the six scenarios in Table 1. The dots represent the mean error across 100

319 simulated datasets, and the error bars depict the 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles.

### 320 UKBMS case study

- 321 Identifying the variables in A
- 322 The experts provided different perspectives on the causes and effects of *R* (UKBMS site inclusion
- 323 including WCBS sites) and Y (the abundances of the meadow brown and small pearl-bordered
- 324 fritillary). Their feedback is provided in full in supplementary materials one and two. Fig. 3 shows the
- 325 causal diagram reflecting expert two's knowledge of the causes and effects of R and the Y in the case
- 326 of the small pearl-bordered fritillary.



328 Figure 3. Causal diagram depicting causes and effects of sample inclusion in the UK Butterfly

- 329 Monitoring Scheme (*R*) and the abundance of the small pearl-bordered fritillary (*Y*). The diagram
- reflects the knowledge of a taxon and UKBMS expert (expert two). N\_dep is nitrogen deposition,
- 331 mean\_T\_wet\_Q is the mean temperature of the wettest quarter of the year, elev is elevation, bl\_wood
- is broadleaved woodland, protected is the proportion of each grid square that is some form of
- protected area and variables suffixed by "\_quality" denote the proportion of each grid square that is
- both the relevant land cover type (indicated by the rest of its name) and managed appropriately for the
- 335 species. The other variables are self-explanatory.
- A major difference between the two experts' feedback is that expert two indicated positive effects of
- 337 several land cover classes (habitats) on *Y* conditional on the way that they are managed. That is, the
- habitats support high abundances of the species, but only if they are managed appropriately. We
- codified these conditional effects in the causal diagrams by introducing new, *unobserved* variables.
   One is "management", which indicates whether the habitat is managed appropriately for the species,
- and the others are variables that denote the proportion of each site that is both the relevant land cover
- 342 class and managed appropriately (i.e. "good" quality). For example, the expert indicated that heather
- 343 grassland has a positive effect on the abundance of the small pearl-bordered fritillary conditional on
- 344 appropriate management. In the causal diagram, the effect of heather grassland on Y is heather
- 345 grassland  $\rightarrow$  quality heather grassland  $\rightarrow Y$ , where management also has a direct effect on quality
- heather grassland (Fig. 3). Note that we did not specifically ask the experts to provide information on
- 347 conditional effects, which is why expert one did not.

- 348 From each of the four causal diagrams—one for each species and expert—we identified the minimal
- adjustment set A (the variables on which R and Y are hopefully conditionally independent) using the rules of d-separation (Table 2). For each diagram, it is possible to d-separate R and Y without having
- to adjust for any of the unobserved variables introduced to depict the conditional effects of land cover
- 352 classes on *Y* (i.e. management or "quality" habitats). For both species, the variables in *A* differ
- between experts, which meant that two superpopulation models had to be fitted for each one.
- Table 2. Minimal adjustment sets derived from the experts' knowledge for each species. The
- 355 adjustment set need not include all predictors of the species' abundances.

Expert	Species	Minimal adjustment set
1	meadow brown	Calcareous grassland
1	small pearl-bordered fritillary	Broadleaved woodland
2	meadow brown	Calcareous grassland and elevation
2	small pearl-bordered fritillary	Broadleaved woodland, calcareous bedrock and heather

### 357 *Current versus new model outputs*

358 We compared the superpopulation models' outputs to those of the current UKBMS GLM in terms of 359 the annual estimates and the long-term trend, which is the coefficient from a regression of annual

360 index on year (Figs 4 and 5). For both species, the outputs of the superpopulation models are

361 markedly different to those of the UKBMS method. For the meadow brown, the two superpopulation

marked y different to those of the UKBMS method. For the meadow brown, the two superpopulation models (one for each expert) agree that there has been a decline in abundance, whereas the UKBMS

362 models (one for each expert) agree that there has been a deemic in abundance, whereas the OKDINS 363 method suggests that abundance has been stable over time. For the small pearl-bordered fritillary, the

364 current UKBMS method suggests a decline in abundance over time, whereas the two superpopulation

365 models indicate a slight increase.

366 The estimates from one of the two superpopulation models (SM\_2) for the small pearl-bordered

367 fritillary appear to be very uncertain (Fig. 5). This uncertainty is a result of the fact that we rescaled

the estimates in each year by subtracting the estimate from the reference year, 1976. In 1976, there

369 were only eight grid squares with data on the small pearl-bordered fritillary, so the variance in this

370 year is truly large. Subtracting these highly variable estimates from the estimates for subsequent years 371 makes them appear similarly uncertain. The variance of the estimates on the absolute scale is far

371 makes them appear similarly uncertain. The variance of the estimates on the absolute scale is far 372 smaller (supplementary material three; Fig. S4), but we chose to present the estimates relative to 1976

373 for consistency with the UKBMS approach.



374

Figure 4. Time trends in the annual indices of abundance for the meadow brown produced by the current UKBMS GLM (UKBMS), the superpopulation model based on expert one's knowledge (SM\_1) and the superpopulation model based on expert two's knowledge (SM\_2). The left panel shows the time-series, and the right panel shows the estimated trends, which are the coefficients from a regression of index value on year. The uncertainty in both panels was derived by bootstrapping across sites. The vertical lines in the right-hand panel represent the median slopes.





382 Figure 5. Time trends in the annual indices of abundance for the small pearl-bordered fritillary

produced by the current UKBMS GLM (UKBMS), the superpopulation model based on expert one's knowledge (SM 1) and the superpopulation model based on expert two's knowledge (SM 2). The left

panel shows the time-series, and the right panel shows the estimated trends, which are the coefficients

from a regression of index value on year. The uncertainty in both panels was derived by bootstrapping

across sites. The break in the Y axis on the left panel was introduced to show the full uncertainty in
 SM 2 whilst also enabling comparison of the three models. The vertical lines in the right-hand panel

represent the median slopes.

### 390 Discussion

391 We have demonstrated how causal diagrams and superpopulation models might be used to estimate

392 the landscape-wide mean of some variable of interest *Y* (e.g. a species' abundance or occupancy) from

393 geographically biased monitoring data. Our simulations show that, if the variables that explain the

- 394 geographic bias (i.e. *A*) are measured (without error), known and included in the superpopulation
- 395 model, then that model is unbiased (Fig. 2). Clearly, these ideal conditions are unlikely, a point we 396 come back to below. By fitting models for multiple time-periods, we estimated time trends in the
- mean relative abundances of two species of butterfly using data from the UKBMS. The trends are
- different to those estimated using the UKBMS's existing method, which does not adjust for
- 399 geographic bias (Figs 4 and 5).

400 The experts (redacted) were not confident about whether the superpopulation models more accurately

- 401 captured the UK-wide trends for the two species than the existing UKBMS method. The UKBMS
- 402 conducts a regional breakdown of each species' trend in the UK (https://ukbms.org/official-statistics).
- 403 For the small pearl-bordered fritillary, it reports a strong decline in England but a strong increase in
- 404 Scotland. Scotland is relatively underrepresented in the UKBMS data, so a good adjustment should
- 405 place more weight on the trend in this region. The superpopulation models clearly give more weight
- 406 to the Scottish trend than the UKBMS method—one even suggests that the species is increasing at the
- 407 UK level. Nevertheless, two experts (redacted) are sceptical that the small pearl-bordered fritillary is
- 408 not declining at the UK level (based on e.g. an observed decline in its distribution). All experts felt
- 409 that the superpopulation model estimates for the meadow brown are plausible (although none were
- 410 highly confident). Their reasoning is that the species is probably doing better or at least as well at
- 411 sampled than at non-sampled locations.
- 412 From a theoretical perspective, there are some limited cases in which the UKBMS model and others
- 413 like it could capture the true trend in the landscape-wide mean of a species' abundance *Y* despite not
- adjusting for geographic biases. If, for example, the bias is time-invariant in terms of both sign and
- 415 magnitude, then no adjustment is needed. This scenario is highly unlikely, however. The distribution
- 416 of sample inclusion *R* changes over time, because different sites are sampled in different years. So too
- 417 does the distribution of *Y* unless the focal species' relative abundance remains the same at each site in
- 418 each time-period, which is clearly implausible. As the distributions of R and Y change over time, it is

- 419 highly unlikely that the correlation between the two, i.e. the bias, would remain constant. We also
- 420 note that the existing UKBMS model could produce unbiased estimates of alternative estimands using
- 421 the UKBMS data. For example, one might be interested in the trend in the mean abundance across
- 422 occupied sites (i.e. where  $Y \ge 1$ ), in which case sampling all populations would permit unbiased
- 423 inference. Of course, this would require knowing the locations of all populations, and range shifts
- 424 would complicate matters.

425 The major benefit of using superpopulation models rather than conventional methods (e.g. a GLM

- 426 with site and year effects) is that they relax the highly untenable assumption that there is no
- 427 geographic bias; instead, they work on the weaker and slightly more tenable assumption that there is
- 428 no geographic bias conditional on the adjustment set *A*. Of course, satisfying this weaker assumption
   429 means being confident that i) experts were able to identify all relevant causes and effects of sample
- 427 inclusion R and the variable of interest Y and that ii) data on those variables are available, which are
- 431 doubtful. The hope is that the models have reduced the geographic bias, i.e. the correlation between R
- 432 and Y, to the point where the adjusted estimates of the landscape-wide mean of Y are appreciably less
- 433 biased than the naïve ones.
- 434 Whether a superpopulation model estimate of the landscape-wide mean of Y is less biased than a naïve (i.e. unadjusted) one depends on several factors, some of which were captured by our 435 436 simulations. Where data on all A are available, but they were measured with error, the adjustment 437 should reduce but not eliminate bias (Fig. 2). Matters are more complex where some variables in A 438 are omitted from the model and/or where some variables that are not in A are erroneously included 439 (both of which may result from mis-specifying the causal diagram). Erroneously included/omitted 440 variables that are more strongly related to R and Y have greater potential to cause a bias, because they 441 can induce a larger correlation between the two (Collins et al., 2001; Thoemmes & Rose, 2014). 442 However, the sign of the relationships is also relevant: if one erroneously omitted/included variable 443 induces a negative geographic bias and another induces a positive one, then the two might cancel each 444 other out and cause no bias (Thoemmes & Rose, 2014). Our simulations do not capture the effects of 445 mis-specifying the causal diagrams, because any choice of a select few scenarios of strengths and 446 directions of effects and causal diagram structures would have been necessarily arbitrary, but analysts 447 should recognise that the success of the superpopulation modelling approach is contingent on 448 accuracy of the causal diagram.
- 449 Indeed, constructing accurate causal diagrams is the major practical limitation of our approach.
- Analysts might have hundreds or even thousands of species in mind, and experts might not have the knowledge to construct causal diagrams for each one. Even if they did, it would be a time-consuming exercise (although less costly than full probability sampling, which would be needed to satisfy the assumptions of conventional methods). One option for reducing this burden might be to identify and adjust for a set of variables that have large causal effects on *R* and *Y* for many species: for example, woodland in the case of woodland birds or grassland in the case of grassland butterflies. Such a strategy is likely to miss important variables in *A* for some species, however, so it should only be used
- 450 strategy is likely to miss important variables in T for some species, however, so it should only be use 457 as a last resort. Another option might be to crowd-source information on the causes and effects of R
- 458 and *Y* from taxon and dataset experts. This strategy could work well for well-studied taxa such as 459 butterflies, birds and mammals, but it will be more challenging for species whose autecology is less
- 460 understood. It might also yield feedback from more than two experts per species (as here), which
- 461 would be desirable.
- 462 Another question is how comprehensive the causal diagrams need to be. It might be sufficient to 463 include direct causes of R and Y and the causal links among those variables as we did here. However, there is a risk that including additional variables in the diagram, which do not do not directly affect R 464 465 or Y, might reveal paths between them. For example, imagine the diagram broadleaved woodland  $\rightarrow$ R; heather grassland  $\rightarrow Y$ . According to this diagram, R and Y are independent, and there is no 466 geographic bias. Now suppose that we construct a more comprehensive diagram that includes annual 467 468 temperature as a cause of both broadleaved woodland (say, density) and heather grassland. Extending 469 the diagram in this way reveals a path (i.e. a correlation) between Y and R that would have been 470 missed by including only direct causes of the two, and it would change the adjustment set A. Omitting

- 471 variables whose effects on R and Y are indirect is less problematic than omitting proximal ones,
- because indirect causes necessarily explain less of the variation in the two (Grace & Irvine, 2020). 472
- 473 Nevertheless, analysts should acknowledge that a more comprehensive causal diagram is more likely
- 474 to yield the true set of variables in A, and this must be balanced against the increased effort required to
- 475 construct it (also noting that a more comprehensive diagram might result in a more complex
- 476 superpopulation model, which could increase its variance).
- 477 Having identified the variables in A, superpopulation models are just one of several methods that
- 478 could be used to adjust for them (Boyd, Stewart, et al., 2023). Alternatives include inverse probability
- 479 weighting (Fink et al., 2023; Johnston et al., 2020), poststratification (Van Swaay et al., 2002) and
- 480 others. Each of these methods can be recast mathematically as a means to eliminating the correlation between R and Y (Meng, 2022), but, crucially, they are only guaranteed to achieve this goal where the
- 481
- 482 variables in A have been identified correctly (Bailey, 2022).
- 483 Alternative methods exist that do not require complete knowledge of or data on the variables in A, but
- 484 their assumptions are challenging if not impossible to evaluate. It is becoming common to model
- geographic bias using spatial random fields, for example, which assign a value of sampling intensity 485
- to every location in the landscape based on spatial autocorrelation in the sampling locations (e.g. 486
- 487 Simmonds et al., 2020). Use of this approach essentially substitutes the assumption that R and Y are
- 488 independent given A for the assumption that they are independent given the spatial field and other
- 489 covariates in the model (Diggle et al., 2010). Whether this assumption holds depends on whether the 490
- true variables in A exhibit a consistent pattern of spatial autocorrelation across the landscape, which is
- 491 not possible to verify without first identifying those variables.
- 492 It might seem like using causal diagrams and superpopulation models to estimate time trends in
- 493 species' abundances requires stronger assumptions than traditional approaches (e.g. the GLM used by
- 494 the UKBMS). Importantly, however, these non-parametric assumptions are codified explicitly in the
- 495 form of causal diagrams (although parametric assumptions such as linear effects of covariates are
- 496 not), whereas the assumptions of simpler approaches are often overlooked. When the goal is to draw 497 landscape-scale inferences, using a model that does not adjust for geographic bias means assuming
- 498 that it does not exist. Not only is this assumption untenable (we know that the UKBMS' and other
- 499 biodiversity data are geographically biased), but it has the potential to introduce substantial estimation
- 500 error if violated. As they make different assumptions, superpopulation models can be fitted in addition
- to conventional models as part of a sensitivity analysis (as in this paper). They can also be used as the 501
- 502 primary method of analysis where there is clear risk of bias (Boyd et al., 2022).
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- Data availability: The butterfly data must be requested from the UK Butterfly Monitoring Scheme at 510

511 https://ukbms.org/request-data. All code used to conduct our analyses are provided in the

- supplementary materials. We will deposit the code on Zenodo should the article be accepted for 512
- 513 publication.

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