

# On the trade-off between accuracy and spatial resolution when estimating species occupancy from biased samples

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## Abstract

Species occupancy is often defined as the proportion of areal units (sites) in a landscape that the focal species occupies, but it is usually estimated as the proportion of *sampled* sites in which the species has been observed. Assuming perfect detection (i.e. no false absences), we show that three quantities—the degree of sampling bias (in terms of site selection), the proportion of sites that have been sampled and the variability of true occupancy across sites—determine the extent to which a sample-based estimate of occupancy differs from the truth. That these are the only three quantities to affect the accuracy of estimates of species occupancy is the fundamental insight of the “Meng equation”, an algebraic re-expression of statistical error. We use simulations to show how each of the three quantities vary with the spatial resolution of the analysis and that actual estimation error is lower at coarser resolutions. Although finely resolved estimates of species occupancy have the potential to be more useful than coarse ones, this potential is only realised if the estimates are at least reasonably accurate. Consequently, wherever there is the potential for sampling bias, there is a trade-off between spatial resolution and accuracy, and the Meng equation provides a theoretical framework in which analysts can consider the balance between the two.

**Key words:** sampling bias; spatial grain; representativeness; biodiversity monitoring

## Introduction

Species occupancy, which we define as the proportion of areal units (sites) in some defined landscape occupied by the focal species, is often of interest to ecologists (Kéry & Royle, 2016). It is used to quantify species' range dynamics (Dennis et al., 2019; Outhwaite et al., 2020; Powney et al., 2019; Stroh et al., 2023), identify correlates and drivers of those range dynamics (Cooke et al., 2023; Woodcock et al., 2016), track the spread of invasive species and their effects on native taxa (Roy et al., 2012) and monitor progress towards (inter-) national biodiversity targets (Boyd, August, et al., 2023). Clearly, information on species occupancy has the potential to be useful, but realising this potential is conditional on available data being an accurate reflection of reality.

A major source of inaccuracy when estimating species occupancy is geographic sampling bias. In most circumstances—and particularly at fine scales across large areas—it is not possible to sample all sites, so occupancy must be estimated from the subset of sites that have been sampled (Kéry & Royle, 2016). If occupancy differs between sampled and non-sampled sites, then the sample is not representative, and the sample-based estimate of species occupancy will differ from its true value in the wider landscape (Boyd, Powney, et al., 2023; Meng, 2018). Sampling biases are just one of many sources of error when estimating species occupancy (e.g. Isaac et al., 2014; MacKenzie et al., 2002).

Further complicating estimation of species occupancy is that it varies with spatial resolution.

Occupancy always increases as the resolution is coarsened, but the rate at which it increases depends

42 on the fine-scale properties of the species' geographic distribution (Azaele et al., 2012; Kunin, 1998;  
43 Wilson et al., 2004). Occupancy is a better surrogate for abundance, which is often of primary  
44 interest, at fine resolutions (Kunin, 1998). Indeed, where the scale of analysis is roughly the size of an  
45 individual, occupancy and abundance are equivalent. A species' abundance is more variable than its  
46 occupancy (e.g. Dennis et al., 2019), since local occupancy does not decline until local abundance  
47 reaches zero and cannot increase once it is above zero. Consequently, working at finer scales, where  
48 occupancy is a better surrogate for abundance, means having a greater power to detect change.

49 Although estimates of occupancy are nominally more useful at fine scales, there are reasons to work  
50 at coarser resolutions too. One reason is that resourcing constraints might preclude the additional  
51 sampling effort required to estimate occupancy at fine resolutions. Another is that the effects of  
52 sampling biases become more pronounced where there are more sites in the landscape (Boyd,  
53 Powney, et al., 2023; Meng, 2018), which is obviously the case at finer resolutions (i.e. where the  
54 sites are smaller). The fact that sampling biases are more pervasive at finer spatial resolutions raises  
55 questions about how the accuracy of estimates of species occupancy scales with resolution. Although  
56 working at coarser resolutions will clearly improve accuracy at the extremes—we can be surer a  
57 species occupies planet earth than a set of small plots on its surface—how accuracy varies along the  
58 gradient from fine to coarse resolutions under sampling bias has not, to our knowledge, been  
59 investigated in ecology.

60 Here then, we investigate how the error of sample-based estimators of species occupancy vary with  
61 spatial resolution. Assuming no false absences (or that a model has adequately corrected them), we  
62 begin by demonstrating that three, and only three, quantities determine the magnitude of the error: the  
63 degree of sampling bias (in terms of site selection), the proportion of sites sampled and the variability  
64 of true occupancy across sites. That these are the only quantities affecting estimation error is a key  
65 implication of Meng's (2018) decomposition of survey error. We use simulations to show how each  
66 of the three quantities and error vary with spatial resolution under sampling bias (at the finest  
67 resolution) and how varying the level of sampling bias affects the error. A trade-off emerges between  
68 finely resolved and accurate estimates, which we discuss in detail. Analysts should consider our  
69 results when deciding on the most appropriate resolution at which to estimate species occupancy.

## 70 Methods

### 71 Quantifying estimation error

72 We consider a landscape comprising  $N$  sites. The presence of at least one individual of the focal  
73 species is a binary variable  $Y$  taking the value 1 at sites where it is present and 0 elsewhere.  
74 Occupancy  $P(Y = 1)$  is the proportion of sites at which the species is present, which is equivalent to  
75 the mean of  $Y$  across sites  $\bar{Y}$ . Of the  $N$  sites, a subset  $n$  are sampled. Whether each site is one of the  $n$   
76 sampled sites is another binary variable  $R$  ( $R = 1$  where the site is sampled and  $R = 0$  otherwise). It  
77 is not possible to calculate mean occupancy across all  $N$  sites,  $\bar{Y}_N$ , because information is not available  
78 on sites with  $R = 0$ . Instead, it is common to *estimate*  $\bar{Y}_N$  as mean occupancy across sampled sites  $\bar{Y}_n$ .

79 Assuming no measurement error (e.g. false absences), the actual error of  $\bar{Y}_n$  as an estimator of  $\bar{Y}_N$  is  
80 (Meng, 2018)

$$\bar{Y}_n - \bar{Y}_N = \rho(R, Y) \sqrt{\frac{1-f}{f}} \sigma_Y. \quad \text{equation 1}$$

81 The first quantity on the right,  $\rho(R, Y)$ , is the (population) correlation between  $Y$  and  $R$ . It is a  
82 measure of both the sign and magnitude of *sampling bias*. In simple terms,  $\rho(R, Y)$  is negative where  
83  $Y$  is generally smaller in the sample than in the population and vice versa.  $f$  is the sampling rate  
84 ( $n/N$ ), and the second quantity on the right is a measure of *data quantity*. The final quantity  $\sigma_Y$  is the

85 population standard deviation of  $Y$ . It is 0 where  $Y$  is constant, in which case a sample size of 1 is  
86 sufficient to estimate  $\bar{Y}_N$  with no error, and it is largest where  $Y$  is most variable. Hence, it can be  
87 considered a measure of “*problem difficulty*” (Meng, 2018), although we refer to it as occupancy  
88 variability given the context in which we are working.

89 Importantly, eq. 1 gives the actual error of  $\bar{Y}_n$  as an estimator of  $\bar{Y}_N$  for a given sample: that is, for one  
90 realisation of  $R$ . In what follows, we consider replicate realisations of  $R$  from given  $R$ -generating (i.e.  
91 sampling) mechanisms and the average  $\bar{Y}_n - \bar{Y}_N$  across those samples.

## 92 Effects of spatial resolution on error

93 Eq. 1 provides a basis for understanding the effects of resolution on absolute error when estimating  
94 species occupancy. Assuming perfect detection, it implies that there are three, and only three, ways to  
95 reduce error: decrease the sampling bias  $\rho(R, Y)$ , increase the sampling rate  $f$  and/or decrease the  
96 occupancy variability  $\sigma_Y$ . Below we describe a set of simulations that demonstrate the effects of  
97 coarsening the spatial resolution on each of these quantities and on error.

## 98 Simulation setup

### 99 *Virtual landscape, species and samples*

100 The virtual landscape comprises a square grid of  $N = 6400$  cells ( $80 \times 80$ ) at the finest resolution.  
101 Each cell might represent, say, a  $1 \times 1$  km grid square, but the precise definition is not important for  
102 drawing general conclusions.

103 We simulated six species’ geographic distributions, of different sizes and with different levels of  
104 clustering, in the virtual landscape. Our approach was a simplified version of the one used by Guélat  
105 & Kéry (2018). For each species, the first step was to populate every cell in the landscape with an  
106 index  $X$  sampled from a multivariate normal distribution

$$X \sim \mathcal{N}(\boldsymbol{\mu}, \boldsymbol{\delta}), \quad \text{equation 2}$$

107 where  $\boldsymbol{\mu}$  is an  $N$ -vector of 0’s (i.e. mean  $X$  for each grid cell) and  $\boldsymbol{\delta}$  is an  $N \times N$  covariance matrix.  
108 We used an exponential decay function to define the covariance matrix

$$\boldsymbol{\delta} = e^{-\varphi \mathbf{D}_{i,j}}, \quad \text{equation 3}$$

109 where  $\varphi$  is the decay constant and  $\mathbf{D}_{i,j}$  is the Euclidian distance between grid cells  $i$  and  $j$ . Larger  
110 values of  $\varphi$  result in patchier distributions, because the covariance between grid cells diminishes  
111 faster with the distance between them.

112 The next step was to convert the continuous index  $X$  to a binary one (i.e. occupied vs unoccupied)  
113 with a specified proportion of cells being occupied. For each species, we set a threshold percentile of  
114  $X$  across grid cells ( $1 - \bar{Y}_N$ ) above which the cell was designated occupied and below which it was  
115 designated unoccupied. Table 1 lists the parameters used to simulate each species’ geographic  
116 distribution and the resulting properties of those distributions.

117 It was important that the simulated species’ distributions spanned a range of plausible sizes and levels  
118 of clustering, because these properties determine how  $\bar{Y}_N$  scales with resolution (Kunin, 1998). We  
119 tested whether the distributions covered sufficiently wide ranges of these parameters using their  
120 fractal dimensions (Kunin, 1998). The fractal dimension  $D$  of a species’ distribution is given by  $D =$   
121  $2(1 - b)$ , where  $b$  is the slope of its scale-area curve (i.e. a plot of the logarithm of range size against  
122 the logarithm of the area of each grid cell; Hartley & Kunin, 2003). We calculated  $b$  over the finest  
123 three resolutions, because for the medium and common species, including the coarsest two resolutions  
124 resulted in nonlinear scale-area curves (i.e. their distributions are non-fractal at coarse scales). The  
125 theoretical limits of the fractal dimension are 0, representing a species whose distribution is very

126 sparse, and 2, representing a species whose distribution is very clustered (Hartley & Kunin, 2003).  
 127 Our virtual species' distributions spanned the majority of this range (0.31–1.64). Note that  $D$  is  
 128 positively related to  $\bar{Y}_N$  (Wilson et al., 2004).

129 Table 1. Properties of the six virtual species' distributions at the finest spatial resolution. The  
 130 autocorrelation parameter is the exponential decay constant in eq. 3, and higher values produce a more  
 131 dispersed distribution. The theoretical limits for the fractal dimension are 0, representing a highly  
 132 dispersed species, and 2, representing a very clustered one. The fractal dimension also varies with  $\bar{Y}_N$   
 133 (Wilson et al., 2004).

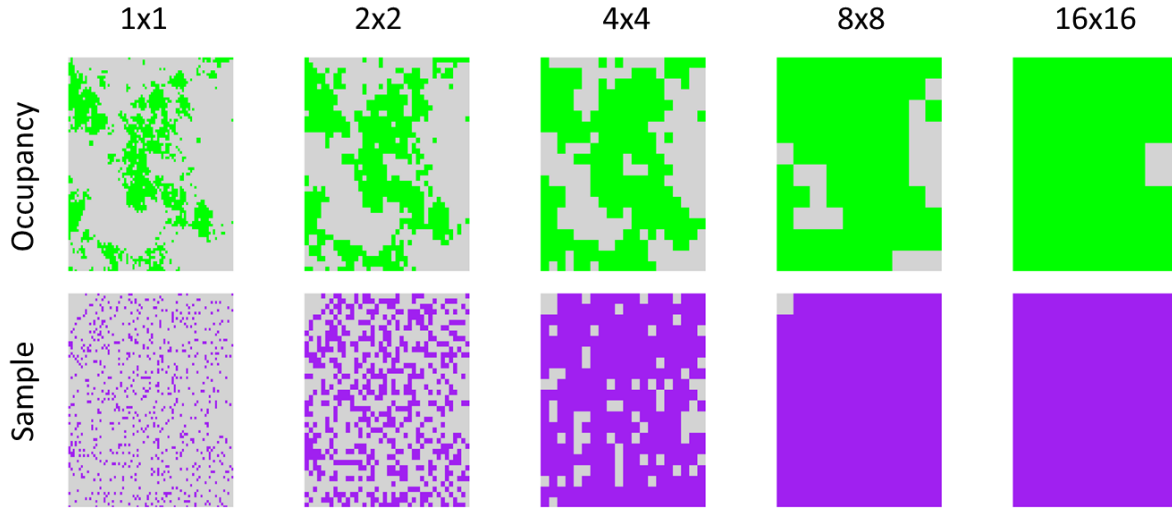
Distribution properties	Exponential decay parameter in autocorrelation function	Proportion of sites occupied (at the finest scale)	Fractal dimension
Rare and sparse	0.6	0.01	0.31
Rare and clustered	0.1	0.01	0.87
Medium and sparse	0.6	0.25	1.20
Medium and clustered	0.1	0.25	1.39
Common and sparse	0.6	0.5	1.57
Common and clustered	0.1	0.5	1.64

134

135 For each species, we simulated 100 virtual samples at the finest resolution. Whilst it might seem more  
 136 logical to simulate one set of samples for all species, this would not allow control over  $\rho(R, Y)$ , the  
 137 sampling bias, which depends on the focal species' geographic distribution. For most simulations, we  
 138 simulated the samples in such a way that  $E_R[\rho(R, Y)] \sim 0.05$  and  $f = 0.1$ , where  $E_R[\rho(R, Y)]$  is the  
 139 expectation (average) of  $\rho(R, Y)$  over the 100 simulated samples (i.e. with respect to  $R$ ). See the  
 140 supplementary Fig. S1 for the distributions of  $\rho(R, Y)$  across samples for each species. We based the  
 141 values of  $\rho(R, Y)$  and  $f$  on an empirical example: a citizen science dataset on vascular plant sampling  
 142 and the species *Calluna vulgaris*' occupancy in Britain (Boyd et al., 2023). Whilst we generally set  
 143  $E_R[\rho(R, Y)] \sim 0.05$  and  $f = 0.1$ , we also demonstrate the effects of varying both parameters (in the  
 144 supplementary material for  $f$ ). Switching the sign of  $\rho(R, Y)$  (i.e. whether occupancy is larger or  
 145 smaller in the sample than the population) would switch the sign of the error in the estimate of mean  
 146 occupancy, but for simplicity we only present the positive case.

#### 147 Analysis of error at each resolution

148 The goal of our analysis was to determine how the actual error of  $\bar{Y}_n$  as an estimator of  $\bar{Y}_N$  ( $\bar{Y}_n - \bar{Y}_N$ ;  
 149 assuming perfect detection) varies with spatial resolution. Starting at the finest resolution, we  
 150 calculated the value of each quantity in eq. 1 (including the actual error; averaged across the 100  
 151 samples). We then coarsened the resolution by aggregating every square of four grid cells into one  
 152 (i.e. doubling the length and width of the site). After coarsening the resolution, we recalculated each  
 153 quantity in eq. 1, coarsened the resolution again and repeated the process until each grid cell was  $16 \times$   
 154 its original height and width. Fig. 1 shows how a species' distribution (medium and clustered; Table  
 155 1) and a sample vary with resolution.



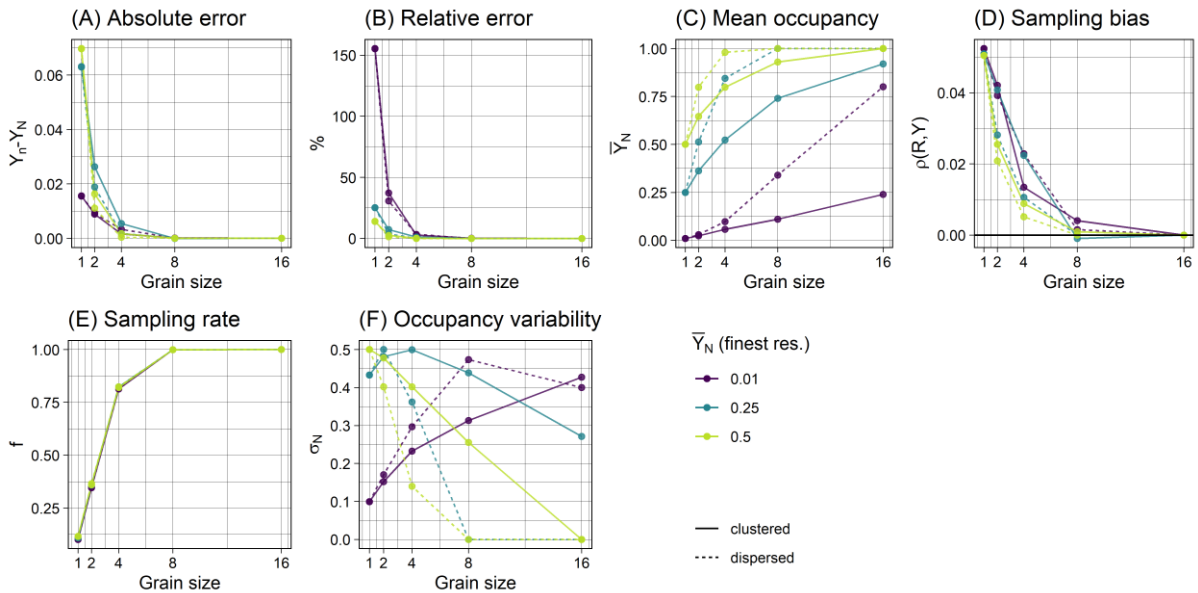
156

157 Figure 1. Top row: a virtual species' ("medium and clustered"; Table 1) geographic distribution at  
 158 each spatial resolution. Green cells are occupied, and grey cells are not. Bottom row: a virtual sample  
 159 at each resolution.  $\rho(R, Y) \sim 0.05$  and  $f \sim 0.1$  at the finest resolution ( $1 \times 1$ ). Purple cells are sampled,  
 160 and grey cells are not. Sampled cells may be either occupied or not.

161 **Results**

162 **Error**

163 For all virtual species, estimates of occupancy are more accurate at coarser resolutions. This is evident  
 164 both in terms of the absolute actual error (Fig. 2A), which is on the left side of eq. 1, and the relative  
 165 actual error (Fig. 2B), which expresses the absolute error as a percentage of true occupancy. Relative  
 166 error is larger for rare species. Absolute error is larger for the medium and common species,  
 167 particularly at the finer resolutions.



168

169 Figure 2. (A) absolute error, (B) relative error (i.e. the absolute error expressed as a percentage of true  
 170 occupancy), (C) mean occupancy (i.e. true occupancy), (D) sampling bias, (E) sampling rate and (F)  
 171 occupancy variability  $\sigma_Y$  at each resolution. The resolution is the height and width of the grid cells in  
 172 arbitrary units. Points represent the average of each statistic over 100 simulated samples. At the finest  
 173 resolution,  $\rho(R, Y) \sim 0.05$  and  $f \sim 0.1$ , the target values for the simulations.

## 174 True occupancy

175 Although well-documented (Azaele et al., 2012; Kunin, 1998), it is worth revisiting the scaling  
176 properties of  $\bar{Y}_N$  (i.e. a species' true occupancy) here, because they provide insight into the scaling  
177 properties of error.  $\bar{Y}_N$  always increases with resolution, but the rate at which it increases depends on  
178 the properties of the species' distribution at the finest resolution (Fig. 2C). Species that are common  
179 and sparsely distributed at the finest resolution quickly reach  $\bar{Y}_N = 1$  as the resolution is coarsened.  
180 By contrast, species that are rare and clustered at the finest resolution do not reach  $\bar{Y}_N = 1$  at any of  
181 the resolutions we considered (Fig. 2A).

## 182 Sampling bias

183 In our simulations, the sampling bias  $\rho(R, Y)$  tends towards 0 as the resolution is coarsened. There are  
184 plausible scenarios in which it will not, however, a point that we expand on in the Discussion.

## 185 Sampling rate

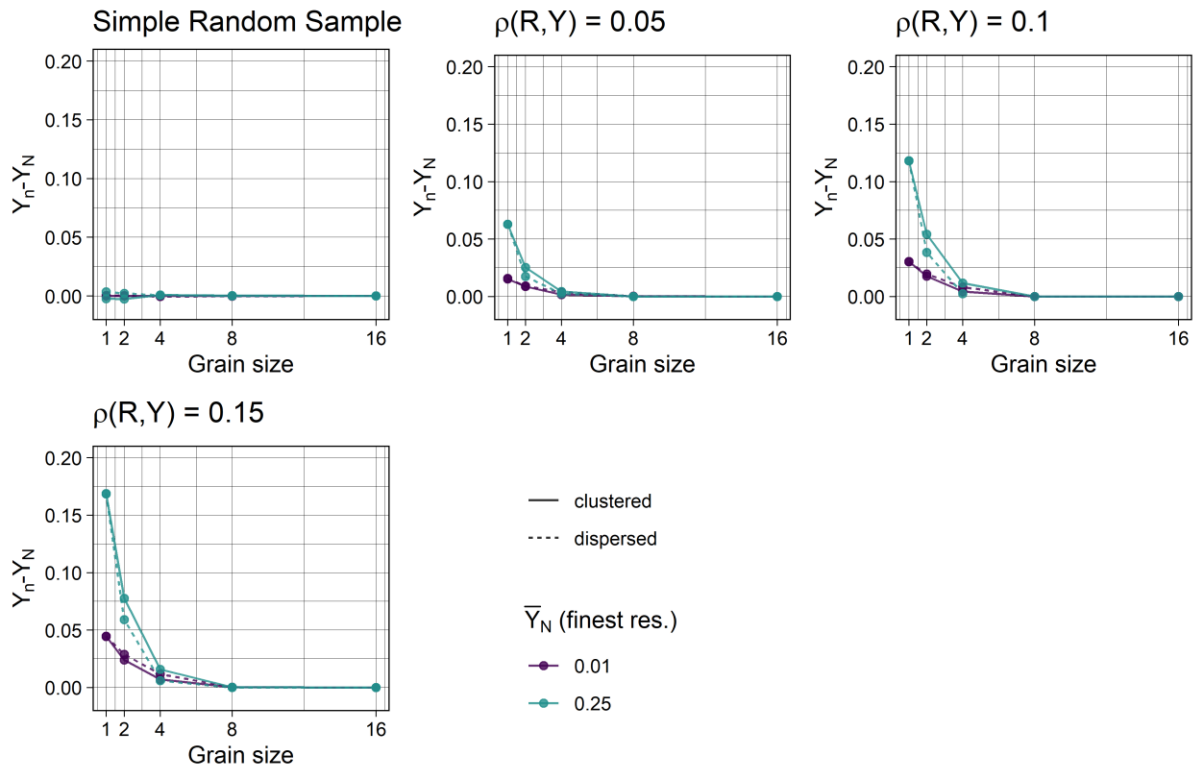
186 The sampling rate  $f$  scales in a similar way with resolution to  $\bar{Y}_N$ . It always increases with resolution,  
187 and sparser samples increase at a greater rate. In our simulations, sparser samples are slightly more  
188 likely for the sparsely distributed species, because we forced a correlation between the species'  
189 distributions and the samples (i.e. a sampling bias). Hence,  $f$  does not increase at exactly the same  
190 rate for all species.

## 191 Occupancy variability

192 As occupancy is binary,  $\sigma_Y = \sqrt{\bar{Y}_N(1 - \bar{Y}_N)}$  (Bradley et al., 2021). It is largest where  $\bar{Y}_N$  is near 0.5  
193 and smallest where  $\bar{Y}_N$  is near 0 or 1. Given that  $\bar{Y}_N$  increases with resolution (Fig. 2C), coarsening the  
194 resolution for species with  $\bar{Y}_N < 0.5$  increases  $\sigma_Y$  until  $\bar{Y}_N = 0.5$  (Fig. 2F). Further coarsening the  
195 resolution decreases  $\sigma_Y$ , because  $\bar{Y}_N$  moves away from 0.5 and towards 1. For species with  $\bar{Y}_N \geq 0.5$   
196 at the finest resolution, coarsening the resolution always decreases  $\sigma_Y$ .

## 197 Scaling of error with resolution at different levels of sampling bias

198 In most simulations, we set  $\rho(R, Y) \sim 0.05$  at the finest resolution, but it is instructive to see how  
199 actual error scales with resolution under different levels of sampling bias. Error generally scales in the  
200 same way with resolution regardless of the level of sampling bias, but is greater in magnitude under  
201 stronger sampling bias (Fig. 3). Under a simple random sample at the finest resolution, where the  
202 expected sampling bias  $E_R[\rho(R, Y)] = 0$ , there is roughly no error at any resolution (recalling that we  
203 present the average error across samples, which essentially removes sampling error). Note that we  
204 were not able to simulate highly biased samples ( $E_R[\rho(R, Y)] \sim 0.15$ ) for the common species (blue  
205 lines in Fig. 3). For these species,  $\bar{Y}_N$  is very different to  $f$ , which makes a large and positive  $\rho(R, Y)$   
206 highly unlikely, and our algorithm for generating the samples could not achieve it.



207

208 Figure 3. Absolute error at each resolution under four levels of sampling bias  $\rho(R, Y)$  (at the finest  
 209 resolution). The resolution is the height and width of the grid cells in arbitrary units. The simple  
 210 random sample has approximately no sampling bias at the finest resolution. Each line represents one  
 211 virtual species: red = rare, green = medium and blue = common. Solid lines depict species with  
 212 clustered distributions at the finest resolution and dashed lines indicate species that are highly  
 213 dispersed at the finest resolution. Points represent the average of each statistic over 100 simulated  
 214 samples.  $f \sim 0.1$  at the finest resolution in all cases.

## 215 Discussion

216 Nobody would dispute the fact that estimates of species occupancy are more accurate at coarse scales  
 217 asymptotically: we can be surer that a species occupies Britain than it does some 1 km grid square  
 218 therein. Our contribution has been to show that accuracy varies somewhat predictably along the  
 219 spectrum from fine to coarse resolutions. Indeed, Meng’s (2018) three-part decomposition provides a  
 220 clear theoretical framework within which analysts can consider quantities like the potential sampling  
 221 bias and the sampling rate when deciding on the appropriate resolution at which to estimate  
 222 occupancy. Coarsening the resolution will be particularly beneficial where sampling biases are likely  
 223 to be large (e.g. when using citizen science data; Pescott et al., 2019, Stroh et al., 2023).

224 The Meng (2018) equation tells us that to increase the accuracy of estimates of species occupancy, we  
 225 should work at the spatial resolution at which the sampling bias and the variability of occupancy in  
 226 the landscape are smallest and at which the sampling rate is highest. Maximising the sampling rate is  
 227 simplest, because it always increases with resolution. The effect of resolution on the variability of  
 228 occupancy in the landscape depends on the species’ prevalence (i.e.  $\bar{Y}_N$ ) at the finest resolution. If  
 229 there is good reason to think that  $\bar{Y}_N \geq 0.5$ —say, from an expert drawn range map—then coarsening  
 230 the resolution will always reduce  $\sigma_Y$ . On the other hand, if there is good reason to think that the  
 231 species is rare, then coarsening the resolution will increase  $\sigma_Y$  until the  $\bar{Y}_N$  reaches 0.5. The effect of  
 232 spatial resolution on sampling bias  $\rho(R, Y)$  is the most difficult to assess of the three quantities that  
 233 determine error.

234 In our simulations,  $\rho(R, Y)$  generally decreased as the spatial resolution was coarsened, but this will  
235 not be universally true. Recall that we presented the average  $\rho(R, Y)$  across 100 samples: for some of  
236 the individual samples,  $\rho(R, Y)$  occasionally increased from one resolution to the next. More general  
237 insight into how  $\rho(R, Y)$  might scale with resolution in other situations can be gleaned from the  
238 formula for Pearson's correlation coefficient.  $\rho(R, Y)$  is the Pearson's correlation between  $R$  and  
239 occupancy  $Y$ , which is to say their covariance divided by the product of their standard deviations. We  
240 have already seen that coarsening the resolution of analysis increases the standard deviation of  $Y$   $\sigma_Y$   
241 until  $\bar{Y}_N \geq 0.5$ , at which point further coarsening the resolution reduces it. The same logic applies to  
242 the standard deviation of the  $R$ , which is also a binary variable. It follows that the denominator in the  
243 formula for  $\rho(R, Y)$ , the product of the standard deviations of  $Y$  and  $R$ , increases as the resolution is  
244 coarsened to the point where  $\bar{Y}_N \geq 0.5$  and  $P(R = 1) \geq 0.5$ , at which point further coarsening the  
245 resolution reduces it. For a given covariance between occupancy and  $R$  then, coarsening the resolution  
246 of analysis will reduce  $\rho(R, Y)$  where  $\bar{Y}_N \geq 0.5$  and  $P(R = 1) \geq 0.5$ . Further work is needed to  
247 understand how the covariance between occupancy and  $R$  will vary with spatial resolution under  
248 different conditions.

249 Of course, error is not the sole criterion on which analysts should base their decision about the spatial  
250 resolution at which to work, because estimates of species occupancy become less useful at coarse  
251 resolutions (assuming a given level of accuracy). For one, the power to detect change is greater at fine  
252 scales, because trends at some fine scale might not be evident at a coarser one (Jönsson et al., 2021).  
253 Coarsening the resolution of estimation thus stands somewhat in opposition to the principle espoused  
254 by the Convention on Biological Diversity (CBD) that indicators should be sensitive to change  
255 (<https://www.cbd.int/indicators/indicatorprinciples.shtml>; although the CBD also ask for “scientific  
256 soundness” and “policy relevance”, implying minimal error as a strongly desirable property). Other  
257 limitations of working at coarse resolutions are that occupancy is a better surrogate for abundance and  
258 often more relevant to policy at fine scales (Kunin, 1998; Spake et al., 2022), and that modelling the  
259 ecological or data generating processes becomes more difficult where the scale of analysis is much  
260 coarser than the scales at which they operate (but see Hill, 2012). Clearly, there is a trade-off between  
261 the usefulness and accuracy of estimates of species occupancy.

262 Importantly, however, the usefulness of an estimate is conditional on it being at least reasonably  
263 accurate. Imagine a species whose occupancy declines at some fine scale over time. It is sampled in  
264 two time-periods, and the sampling bias is strong in both periods. If the sampling bias switches  
265 direction from negative in the first period to positive in the next, then we may fail to detect the decline  
266 or even spuriously detect an increase (depending on the relative magnitudes of the sampling bias;  
267 Bowler et al., 2022; Pescott et al., 2019). Working at a coarser resolution might reduce the error in  
268 both time-periods to the point where the actual trend (at the coarser scale) is detectable and the chance  
269 of detecting a spurious trend is low. Of course, if the sampling bias has the same sign in both time-  
270 periods, then we may be able to detect the decline at the fine resolution despite under- or  
271 overestimating occupancy in both periods (Pocock et al., 2023). Ultimately intuition about the  
272 likelihood of such scenarios requires familiarity with the species' datasets being used for an analysis  
273 and clear assessments of the likely risk of bias (Boyd et al., 2022; Boyd, Powney, et al., 2023).

274 A good example of the potential for bias being balanced against the desire for finely-resolved  
275 estimates of species occupancy is found in the latest plant atlas of the Botanical Society of Britain and  
276 Ireland (Stroh et al., 2023). The data were analysed at a  $10 \times 10$  km scale—much coarser than the  $1 \times$   
277  $1$  km resolution used by others in the area (e.g. Boyd, August, et al., 2023)—and particular time-  
278 periods were omitted, because of serious concerns about sampling biases affecting species data at  
279 finer scales across the 20<sup>th</sup> century. For example, rarer and more critical taxa were more likely to be  
280 reported at finer scales in the early part of the time series. Moreover,  $f$  was known to be far smaller at  
281 smaller scales in these earlier periods (Pescott et al., 2019).



282 Like all simulations, ours are a simplification of reality, which might have implications for the wider  
283 applicability of our results. We did not account for the fact that additional data tend to be available at  
284 coarser resolutions; for example, digitised specimens may be resolved only to some vague locality,  
285 and historic distribution data from species' Atlases tend to be more coarsely resolved than  
286 contemporary data (Groom et al., 2018; Kunin et al., 2000; Pescott et al., 2019). These additional data  
287 would increase the sampling rate  $f$  at coarse resolutions, which, as we have shown, would be likely to  
288 increase the accuracy of sample-based estimates of mean occupancy. [Note that it is possible to  
289 combine fine and coarse data using integrated distribution models and to draw inferences at the finer  
290 scale (Pacifici et al., 2019). Whether the fact that data might be available solely at coarse scales for  
291 historic time-periods, and at multiple scales for recent ones, will impact inference is an open question.  
292 Moreover, it is worth noting that the parameters of any such integrated model will also be subject to  
293 potential biases in estimation in the face of important unmodelled sampling variation.] Our  
294 assumption of perfect detection (i.e. no false absences) is also unrealistic, so it is worth considering  
295 whether the prevalence of false absences is likely to be lower at fine or coarse resolutions. On the one  
296 hand, if a coarse resolution is chosen when planning data collection, false absences might be higher if  
297 the portions of the larger cells that are sampled are not suitable for the focal species (Altwegg &  
298 Nichols, 2019). On the other, if the resolution is chosen at the analysis stage, coarsening the spatial  
299 resolution increases the number of sampling events per grid cell, so, all else being equal, it is more  
300 likely that the focal species will be detected if it is present.

301 Rather than accepting false absences, it is common practice to try to correct them using some sort of  
302 occupancy-detection model (MacKenzie et al., 2002; Royle, 2006). Coarsening the resolution of the  
303 analysis risks violating the closure assumption of occupancy-detection models (Altwegg & Nichols,  
304 2019; Jönsson et al., 2021), but also increases the amount of repeat visits to the same site, which are  
305 needed to estimate detectability and correct false absences. Interesting possibilities are that multi-scale  
306 occupancy models (Mordecai et al., 2011), which relax the closure assumption, could be used and that  
307 fine-scale sampling events could be used as spatial replicates to estimate detection probabilities and  
308 correct false absences at coarser scales (cf. Srivathsa et al., 2018). While failing to correct false  
309 absences can make estimates of species occupancy worse, it is important to remember that  
310 successfully correcting them only reduces error to its baseline level determined by sampling biases  
311 (Meng, 2018).

312 Coarsening the resolution of an analysis is one approach to counter some of the error introduced by  
313 sampling biases, but there are alternatives. One is to estimate mean occupancy in the population using  
314 a *weighted* sample mean, where the weights are equal to the inverse of the (estimated) sample  
315 inclusion probabilities (Boyd, Stewart, et al., 2023; Johnston et al., 2020). If successful, weighting of  
316 this type brings the distribution of occupancy in the sample closer to its distribution in the population  
317 and can be recast as a means to minimising  $\rho(R, Y)$  (Meng, 2022). Several approaches to estimating  
318 sampling weights for unstructured (i.e. nonprobability) samples, the principal type of data used to  
319 estimate species occupancy, exist (Boyd, Stewart, et al., 2023; Elliott & Valliant, 2017). Weighting is  
320 often more successful where available covariates explain larger portions of the variance in sample  
321 inclusion (i.e.  $R$ ) and the variable of interest (occupancy; Collins et al., 2001), and it would be useful  
322 to investigate how this scales with spatial resolution.

323 Analysts consider several factors when deciding on the appropriate resolution at which to estimate  
324 species occupancy. Examples include the focal species' home range sizes (Wilson & Schmidt, 2015),  
325 the scale at which they use the landscape more generally (Powney et al., 2019), the number of  
326 replicate visits to the same site within closure periods (Outhwaite et al., 2019) and the resolution at  
327 which the data were collected (Higa et al., 2015). We propose that analysts should also consider the  
328 fact that estimates are likely to be more accurate at coarse resolutions, because a highly erroneous  
329 finer-scale estimate is unlikely to be useful for most applications. The Meng (2018) equation provides

330 a theoretical framework in which accuracy and the desire for finely resolved information can be  
331 balanced.

## 332 Code availability

333 All code needed to fully reproduce our analysis is available at  
334 <https://github.com/robboyd/biasVsResolution>.

## 335 References

- 336 Altwegg, R., & Nichols, J. D. (2019). Occupancy models for citizen-science data. *Methods in Ecology*  
337 *and Evolution*, 10(1), 8–21. <https://doi.org/10.1111/2041-210X.13090>
- 338 Azaele, S., Cornell, S. J., & Kunin, W. E. (2012). Downscaling species occupancy from coarse spatial  
339 scales. *Ecological Applications*, 22(3), 1004–1014. <https://doi.org/10.1890/11-0536.1>
- 340 Bowler, D. E., Callaghan, C. T., Bhandari, N., Henle, K., Barth, M. B., Koppitz, C., Klenke, R.,  
341 Winter, M., Jansen, F., Bruelheide, H., & Bonn, A. (2022). Temporal trends in the spatial bias of  
342 species occurrence records. *Ecography*. <https://doi.org/10.1111/ecog.06219>
- 343 Boyd, R. J., August, T., Cooke, R., Logie, M., Mancini, F., Powney, G., Roy, D., Turvey, K., & Isaac,  
344 N. (2023). An operational workflow for producing periodic estimates of species occupancy at  
345 large scales. *Biological Reviews*, 9. <https://doi.org/10.32942/OSF.IO/2V7JP>
- 346 Boyd, R. J., Powney, G. D., Burns, F., Danet, A., Duchenne, F., Grainger, M. J., Jarvis, S. G., Martin,  
347 G., Nilsen, E. B., Porcher, E., Stewart, G. B., Wilson, O. J., & Pescott, O. L. (2022). ROBITT: A  
348 tool for assessing the risk-of-bias in studies of temporal trends in ecology. *Methods in Ecology*  
349 *and Evolution*, 13(March), 1497–1507. <https://doi.org/10.1111/2041-210X.13857>
- 350 Boyd, R. J., Powney, G. D., & Pescott, O. L. (2023). We need to talk about nonprobability samples.  
351 *Trends in Ecology & Evolution*, xx(xx), 1–11. <https://doi.org/10.1016/j.tree.2023.01.001>
- 352 Boyd, R. J., Stewart, G. B., & Pescott, O. L. (2023). Descriptive inference using large ,  
353 unrepresentative nonprobability samples : An introduction for ecologists. *Ecoevorxiv*, April.  
354 <https://doi.org/10.32942/X2359P>
- 355 Bradley, V. C., Kuriwaki, S., Isakov, M., Sejdinovic, D., Meng, X. L., & Flaxman, S. (2021).  
356 Unrepresentative big surveys significantly overestimated US vaccine uptake. *Nature*, 600(7890),  
357 695–700. <https://doi.org/10.1038/s41586-021-04198-4>
- 358 Collins, L. M., Schafer, J., & Kam, C. (2001). A Comparison of Restrictive Strategies in Modern  
359 Missing Data Procedures. *Psychological Methods*, 6(June). <https://doi.org/10.1037/1082-989X.6.4.330>
- 361 Cooke, R., Mancini, F., Boyd, R., Evans, K. L., Shaw, A., Webb, T. J., & Isaac, N. J. B. (2023).  
362 Protected areas support more species than unprotected areas in Great Britain , but lose them  
363 equally rapidly. *Biological Conservation*, 278(December 2022), 109884.  
364 <https://doi.org/10.1016/j.biocon.2022.109884>
- 365 Dennis, E. B., Brereton, T. M., Morgan, B. J. T., Fox, R., Shortall, C. R., Prescott, T., & Foster, S.  
366 (2019). Trends and indicators for quantifying moth abundance and occupancy in Scotland.  
367 *Journal of Insect Conservation*, 23(2), 369–380. <https://doi.org/10.1007/s10841-019-00135-z>
- 368 Elliott, M. R., & Valliant, R. (2017). Inference for nonprobability samples. *Statistical Science*, 32(2),  
369 249–264. <https://doi.org/10.1214/16-STS598>
- 370 Groom, Q. J., Marsh, C. J., Gavish, Y., & Kunin, W. E. (2018). How to predict fine resolution  
371 occupancy from coarse occupancy data. *Methods in Ecology and Evolution*, 9(11), 2273–2284.  
372 <https://doi.org/10.1111/2041-210X.13078>

- 373 Guélat, J., & Kéry, M. (2018). Effects of spatial autocorrelation and imperfect detection on species  
374 distribution models. *Methods in Ecology and Evolution*, 9(6), 1614–1625.  
375 <https://doi.org/10.1111/2041-210X.12983>
- 376 Hartley, S., & Kunin, W. E. (2003). Scale Dependency of Rarity, Extinction Risk, and Conservation  
377 Priority. *Conservation Biology*, 17(6), 1559–1570. <https://doi.org/10.1111/j.1523-1739.2003.00015.x>  
378
- 379 Higa, M., Yamaura, Y., Koizumi, I., Yabuhara, Y., Senzaki, M., & Ono, S. (2015). Mapping large-  
380 scale bird distributions using occupancy models and citizen data with spatially biased sampling  
381 effort. *Diversity and Distributions*, 21(1), 46–54. <https://doi.org/10.1111/ddi.12255>
- 382 Hill, M. O. (2012). Local frequency as a key to interpreting species occurrence data when recording  
383 effort is not known. *Methods in E*, 3(2012), 195–205. <https://doi.org/10.1111/j.2041-210X.2011.00146.x>  
384
- 385 Isaac, N. J. B., van Strien, A. J., August, T. A., de Zeeuw, M. P., & Roy, D. B. (2014). Statistics for  
386 citizen science: Extracting signals of change from noisy ecological data. *Methods in Ecology  
387 and Evolution*, 5(10), 1052–1060. <https://doi.org/10.1111/2041-210X.12254>
- 388 Johnston, A., Moran, N., Musgrove, A., Fink, D., & Baillie, S. R. (2020). Estimating species  
389 distributions from spatially biased citizen science data. *Ecological Modelling*, 422(December  
390 2019), 108927. <https://doi.org/10.1016/j.ecolmodel.2019.108927>
- 391 Jönsson, G. M., Broad, G. R., Sumner, S., & Isaac, N. J. B. (2021). A century of social wasp  
392 occupancy trends from natural history collections: spatiotemporal resolutions have little effect  
393 on model performance. *Insect Conservation and Diversity*, 14(5), 543–555.  
394 <https://doi.org/10.1111/icad.12494>
- 395 Kéry, M., & Royle, J. A. (2016). *Applied hierarchical modelling in ecology: analysis of species  
396 distribution, abundance and species richness in R and BUGS*. Academic press.
- 397 Kunin, W. E. (1998). Extrapolating species abundance across spatial scales. *Science*, 281(5382),  
398 1513–1515. <https://doi.org/10.1126/science.281.5382.1513>
- 399 Kunin, W. E., Hartley, S., & Lennon, J. J. (2000). Scaling down: On the challenge of estimating  
400 abundance from occurrence patterns. *American Naturalist*, 156(5), 560–566.  
401 <https://doi.org/10.1086/303408>
- 402 MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, A. A., & Langtimm, C. A.  
403 (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*,  
404 83(8), 2248–2255. [https://doi.org/10.1890/0012-9658\(2002\)083\[2248:ESORWD\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2)
- 405 Meng, X.-L. (2018). Statistical paradises and paradoxes in big data (I): Law of large populations, big  
406 data paradox, and the 2016 us presidential election. *Annals of Applied Statistics*, 12(2), 685–726.  
407 <https://doi.org/10.1214/18-AOAS1161SF>
- 408 Meng, X.-L. (2022). Comments on the Wu ( 2022 ) paper by Xiao-Li Meng 1 : Miniaturizing data  
409 defect correlation : A versatile strategy for handling non-probability samples. *Survey  
410 Methodology*, 48(2), 1–22.
- 411 Mordecai, R. S., Mattsson, B. J., Tzilkowski, C. J., & Cooper, R. J. (2011). Addressing challenges  
412 when studying mobile or episodic species: Hierarchical Bayes estimation of occupancy and use.  
413 *Journal of Applied Ecology*, 48(1), 56–66. <https://doi.org/10.1111/j.1365-2664.2010.01921.x>
- 414 Outhwaite, C., Gregory, R. D., Chandler, R. E., Collen, B., & Isaac, N. J. B. (2020). Complex long-  
415 term biodiversity change among invertebrates, bryophytes and lichens. *Nature Ecology &  
416 Evolution*. <https://doi.org/10.1038/s41559-020-1111-z>
- 417 Outhwaite, C., Powney, G., August, T., Chandler, R., Rorke, S., Pescott, O. L., Harvey, M., Roy, H.

- 418 E., Fox, R., Roy, D. B., Alexander, K., Ball, S., Bantock, T., Barber, T., Beckmann, B. C., Cook,  
419 T., Flanagan, J., Fowles, A., Hammond, P., ... Isaac, N. J. B. (2019). Annual estimates of  
420 occupancy for bryophytes, lichens and invertebrates in the UK, 1970-2015. *Scientific Data*, 6(1),  
421 259. <https://doi.org/10.1038/s41597-019-0269-1>
- 422 Pacifici, K., Reich, B. J., Miller, D. A. W., & Pease, B. S. (2019). Resolving misaligned spatial data  
423 with integrated species distribution models. *Ecology*, 100(6), 1–15.  
424 <https://doi.org/10.1002/ecy.2709>
- 425 Pescott, O. L., Humphrey, T. A., Stroh, P. A., & Walker, K. J. (2019). Temporal changes in  
426 distributions and the species atlas: How can British and Irish plant data shoulder the inferential  
427 burden? *British & Irish Botany*, 1(4), 250–282. <https://doi.org/10.33928/bib.2019.01.250>
- 428 Pocock, M. J. O., Logie, M., Isaac, N. J. B., Fox, R., & August, T. (2023). The recording behaviour of  
429 field-based citizen scientists and its impact on biodiversity trend analysis. *Ecological Indicators*,  
430 151(April), 110276. <https://doi.org/10.1016/j.ecolind.2023.110276>
- 431 Powney, G. D., Carvell, C., Edwards, M., Morris, R. K. A., Roy, H. E., Woodcock, B. A., & Isaac, N.  
432 J. B. (2019). Widespread losses of pollinating insects in Britain. *Nature Communications*,  
433 10(2019), 1–6. <https://doi.org/10.1038/s41467-019-08974-9>
- 434 Roy, H. E., Adriaens, T., Isaac, N. J. B., Kenis, M., Onkelinx, T., Martin, G. S., Brown, P. M. J.,  
435 Hautier, L., Poland, R., Roy, D. B., Comont, R., Eschen, R., Frost, R., Zindel, R., Van  
436 Vlaenderen, J., Nedvěd, O., Ravn, H. P., Grégoire, J. C., de Biseau, J. C., & Maes, D. (2012).  
437 Invasive alien predator causes rapid declines of native European ladybirds. *Diversity and*  
438 *Distributions*, 18(7), 717–725. <https://doi.org/10.1111/j.1472-4642.2012.00883.x>
- 439 Royle, J. A. (2006). Site occupancy models with heterogeneous detection probabilities. *Biometrics*,  
440 62(1), 97–102. <https://doi.org/10.1111/j.1541-0420.2005.00439.x>
- 441 Spake, R., Barajas-Barbosa, M. P., Blowes, S. A., Bowler, D. E., Callaghan, C. T., Garbowski, M.,  
442 Jurburg, S. D., Van Klink, R., Korell, L., Ladouceur, E., Rozzi, R., Viana, D. S., Xu, W. B., &  
443 Chase, J. M. (2022). Detecting Thresholds of Ecological Change in the Anthropocene. *Annual*  
444 *Review of Environment and Resources*, 47, 797–821. <https://doi.org/10.1146/annurev-environ-112420-015910>
- 446 Srivathsa, A., Puri, M., Kumar, N. S., Jathanna, D., & Karanth, K. U. (2018). Substituting space for  
447 time: Empirical evaluation of spatial replication as a surrogate for temporal replication in  
448 occupancy modelling. *Journal of Applied Ecology*, 55(2), 754–765.  
449 <https://doi.org/10.1111/1365-2664.13005>
- 450 Stroh, P. A., Walker, K., Humphrey, T. A., Pescott, O. L., & Burkmar, R. (2023). *Plant Atlas 2020:*  
451 *Mapping Changes in the Distribution of the British and Irish Flora*. Princeton Univ. Press.
- 452 Wilson, R. J., Thomas, C. D., Fox, R., Roy, D. B., & Kunin, W. E. (2004). Spatial patterns in species  
453 distributions reveal biodiversity change. *Nature*, 432(7015), 393–396.  
454 <https://doi.org/10.1038/nature03031>
- 455 Wilson, T., & Schmidt, J. H. (2015). Scale dependence in occupancy models: Implications for  
456 estimating bear den distribution and abundance. *Ecosphere*, 6(9). <https://doi.org/10.1890/ES15-00250.1>
- 458 Woodcock, B. A., Isaac, N. J. B., Bullock, J. M., Roy, D. B., Garthwaite, D. G., Crowe, A., & Pywell,  
459 R. F. (2016). Impacts of neonicotinoid use on long-term population changes in wild bees in  
460 England. *Nature Communications*, 7. <https://doi.org/10.1038/ncomms12459>

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