**TECHNIQUES & METHODOLOGY**

# A century of social wasp occupancy trends from natural history collections: spatiotemporal resolutions have little effect on model performance

GALINA M. JÖNSSON,[1,2,3,4] ⓘ GAVIN R. BROAD,[1] ⓘ SEIRIAN SUMNER[4] ⓘ and NICK J. B. ISAAC[3] ⓘ [1]Department of Life Sciences, The Natural History Museum, London, UK, [2]Grantham Institute, Imperial College London, London, UK, [3]UK Centre for Ecology & Hydrology, Crowmarsh Gifford, Wallingford, UK and [4]Centre for Biodiversity and Environment Research, University College London, London, UK

**ABSTRACT.** 1. The current dearth of long-term insect population trends is a major obstacle to conservation. Occupancy models have been proposed as a solution, but it remains unclear whether they can yield long-term trends from natural history collections, since specimen records are normally very sparse. A common approach for sparse data is to coarsen its spatial and/or temporal resolution, although coarsening risks violating model assumptions.

2. We (i) test whether occupancy trends of three social wasp (Hymenoptera: Vespidae: Vespinae) species – the common wasp (*Vespula vulgaris*), the German wasp (*Vespula germanica*) and the European hornet (*Vespa crabro*) – have changed in England between 1900 and 2016, and (ii) test the effect of spatiotemporal resolution on the performance of occupancy models using very sparse data. All models are based on an integrated dataset of occurrence records and natural history collection specimen records.

3. We show that occupancy models can yield long-term species-specific trends from very sparse natural history collection specimens. We present the first quantitative trends for three Vespinae species in England over 116 years. *Vespula vulgaris* and *V. germanica* show stable trends over the time series, whilst *V. crabro*'s occupancy decreased from 1950 to 1970 and increased since 1970. Moreover, we show that spatio-temporal resolution has little effect on model performance, although coarsening the spatial grain is an appropriate method for achieving enough records to estimate long-term changes.

4. With the increasing availability of biological records, the model formulation used here has the potential to provide novel insights by making use of natural history collections' unique specimen assemblages.

**Key words.** Bayesian occupancy models, biodiversity, distributions, imperfect detection, long-term trends, natural history collections, presence-only, species occurrence, Vespinae.

## Introduction

Globally declining insect populations have been flagged as a cause for concern by scientists for over a decade (e.g., Conrad *et al.*, 2006; Franzén & Johannesson, 2007;

Harmon *et al.*, 2007; Goulson *et al.*, 2008; Shortall *et al.*, 2009), but have only recently caught the public's attention due to worldwide media coverage in response to alarming new studies. Such studies include Hallmann *et al.* (2017), suggesting that German insect biomass declines exceed 75% over 27 years, and Sánchez-Bayo & Wyckhuys (2019), who warn that 40% of global insect species may become extinct within a few decades. However, although global insect declines are widely acknowledged, such magnitudes are unlikely to represent all insect

species (Cardoso *et al.*, 2019; Goulson, 2019; Hambler & Henderson, 2019; Thomas *et al.*, 2019; Saunders *et al.*, 2020; van Klink *et al.*, 2020; Wagner, 2020). Responding to the continued degradation of insect populations and ecosystem services necessitates robust population trends over long temporal scales as well as large spatial scales, since drivers of change are more likely to be confounded for short-term local changes (Parmesan & Yohe, 2003; Root *et al.*, 2003).

Methods for estimating insect trends traditionally relied on systematically collected data from extensive monitoring schemes, whilst opportunistic presence-only records are the most abundant type of existing biodiversity data (Soberón & Peterson, 2005; Elith *et al.*, 2006; Kissling *et al.*, 2018). Presence-only records detail where and when species were present but lack information about species' absences. As the recording method is rarely known, presence-only records are subject to inherent biases including: irregular recording intensity over time, uneven spatial coverage, varied sampling effort per sampling occasion, and uneven detectability among species and habitats (Isaac & Pocock, 2015). Nonetheless, since presence-only records cover longer time periods than systematically collected data (Troia & McManamay, 2016), they have great potential for estimating long-term changes.

Two types of presence-only records are particularly abundant: firstly, those collected in citizen science projects and species recording schemes, and secondly, specimen records held by natural history collections (Boakes *et al.*, 2010; Kissling *et al.*, 2018). The number of such records is rapidly growing due to natural history collections' increasing commitment to specimen digitisation projects (Graham *et al.*, 2004; Page *et al.*, 2015; Paterson *et al.*, 2016) and a surge in citizen science projects over recent decades (Pocock *et al.*, 2017). The majority of UK species recording schemes were set up after 1970 (Pocock *et al.*, 2015), which postdates by several decades many large-scale transformations of the British landscape (Spencer & Kirby, 1992; Dallimer *et al.*, 2009; Atkinson & Townsend, 2011; Loft *et al.*, 2019). On the other hand, the majority of specimens in museum collections date from the late 1800s to the 1980s (Winker, 2004; Boakes *et al.*, 2010; Brooks *et al.*, 2014; Speed *et al.*, 2018). As different sources of presence-only data vary in temporal coverage, multiple sources can potentially be integrated to produce comprehensive, long-term datasets (Tingley & Beissinger, 2009; Jetz *et al.*, 2012).

Bayesian occupancy models have been shown to produce robust and reliable species trends from presence-only records, even when the data are biased (van Strien *et al.*, 2013; Isaac *et al.*, 2014). Bayesian occupancy models consist of two submodels: a state sub-model estimating occupancy and a detection sub-model estimating detection probability to account for imperfect species detection and inconsistent recording (MacKenzie *et al.*, 2002; Royle & Kéry, 2007). Occupancy models are now routinely used to describe national-scale trends in biodiversity (Cruickshank *et al.*, 2016; Powney *et al.*, 2019; Termaat *et al.*, 2019; van Strien *et al.*, 2019), as well as multispecies biodiversity indicators (Outhwaite *et al.*, 2015; van Strien *et al.*, 2016). To date, occupancy models have rarely been applied to periods before 1970, reflecting that whilst records from recording schemes are often sparse (Outhwaite *et al.*, 2018), natural history collections' specimen records are

even sparser (Boakes *et al.*, 2010; van Strien *et al.*, 2019). Indeed, van Strien *et al.* (2019) argued that most decades of the 20th century had insufficient records of Dutch butterflies to estimate the parameters of an occupancy model. However, Outhwaite *et al.* (2018) showed that certain model specifications make it possible to use sparse data in occupancy models; although the method has not yet been applied to natural history collection specimens.

A common approach to sparse data is to coarsen the spatial and/or temporal resolution of species trends and thereby gain sufficient data for estimating model parameters (e.g., Heessen, 1996; Klapwijk *et al.*, 2013; van Strien *et al.*, 2019). For occupancy models, coarsening either resolution increases the number of records per grid cell and closure period combination (the area and time period over which an occupancy state is estimated; Fig. 1), which theoretically results in more precise estimates of detection probability. However, spatiotemporal coarsening increases the risk of violating the key assumption of occupancy models: no change in occupancy (e.g., through immigration and emigration) within grid cells and closure period combinations (the closure assumption). Hence, there is a trade-off: short closure periods and small grid cells are theoretically best for meeting the closure assumption as they account for fine-scale (meta)population dynamics, whilst long closure periods and large grid cells ensure enough records for estimating detection probability. A remaining question is whether, and to what extent, the closure assumption can be violated by coarsening spatiotemporal resolutions to allow for sparse datasets to be used in occupancy models.

UK social wasps (Hymenoptera: Vespidae: Vespinae) are an ideal model system for exploring questions of long-term change and integrating sparse datasets. There are two main sources of Vespinae presence-only records in the United Kingdom. First, the Bees Wasps and Ants Recording Society (BWARS) collect records based on volunteer and taxonomic expert observations. The majority of records date from 1970 onwards (Fig. 2). Secondly, the Natural History Museum in London (NHM) holds the largest collection of UK Vespinae specimens (see Appendix S1 in the Supporting Information: Table S1.1 for specimen numbers of six British collections) with the majority dating pre-1980 (Fig. 2). BWARS records are considered sparse (Outhwaite *et al.*, 2018) and the NHM records are certainly sparser (Fig. 2), making them suitable for testing whether Bayesian occupancy models can estimate long-term species changes from sparse data.

The common wasp (*Vespula vulgaris*, Linnaeus 1758), the German wasp (*Vespula germanica*, Fabricius, 1793) and the European hornet (*Vespa crabro*, Linnaeus, 1758) all perform important ecosystem services (Sumner *et al.*, 2018), but long-term UK occupancy trends are not well known, and studies of their long-term population dynamics are limited to a few locations in southern England (Archer, 1985, 2001, 2015, 2018; Lester *et al.*, 2017). Through their foraging activity, social wasps contribute to pest control (Richter, 2000; Southon *et al.*, 2019), pollination (Carreck & Williams, 2002) and seed dispersal (Jules, 1996). However, they face numerous threats, including loss of habitat suitable for nesting and agricultural intensification, particularly increased pesticide use (Archer, 2001; Ollerton *et al.*, 2014). *Vespa crabro* has undergone a northwards range expansion in Britain since the 1970s (Bees,
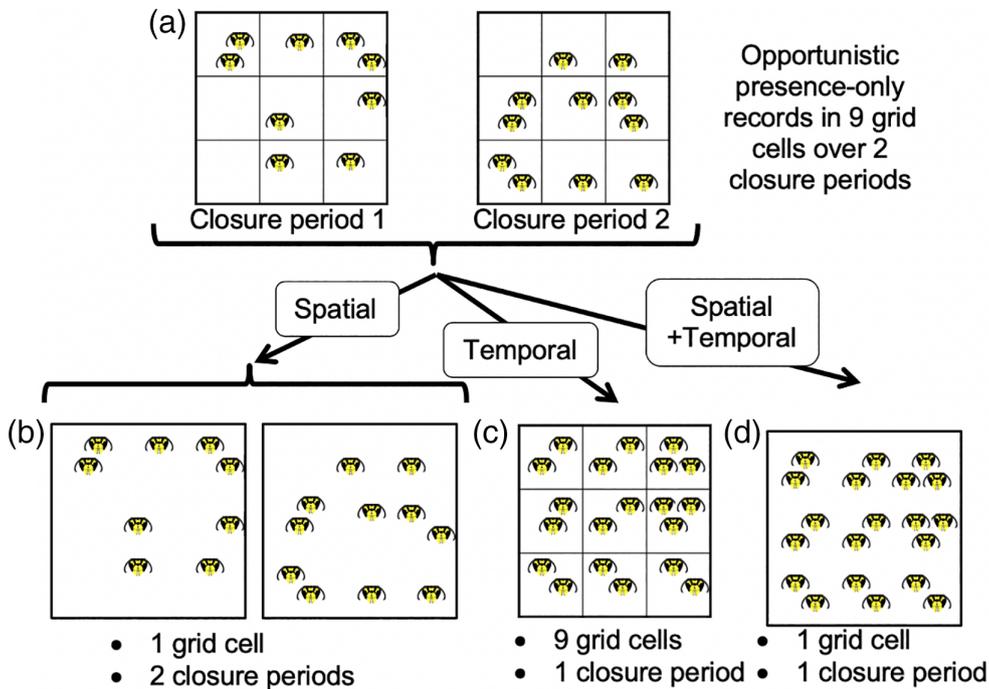
**Figure 1.** Schematic illustrating how (a) sparse presence-only records from nine grid cells over two closure periods can be coarsened to increase the number of records per combination of grid cell and closure period. Data can be (b) spatially coarsened resulting in fewer and larger grid cells, (c) temporally coarsened resulting in fewer and longer closure periods, or (d) both spatially and temporally coarsened resulting in fewer grid cells and closure periods. Squares indicate grid cells. Wasp heads indicate single records. Source: Reproduced with permission from Big Wasp Survey. 2017. *Vespula germanica* head icon. [Image]. Retrieved from https://www.bigwaspsurvey.org/the-wasps/.
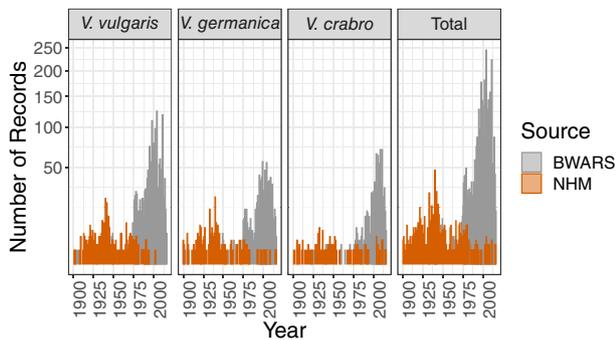


**Figure 2.** The number of *Vespula vulgaris* (*n* = 2053), *Vespula germanica* (*n* = 1089) and *Vespa crabro* (*n* = 935) records used in analyses as well as the total number of records used in analyses (*n* = 4077). All records are from England, date between 1900 and 2016, and are held by the Natural History Museum, London (NHM; grey; *n* = 566) or the Bees, Wasps and Ants Recording Society (BWARS; red; *n* = 3511). Note that the y-axis is plotted on a square root scale.

Wasps & Ants Recording Society, 2019) that has been attributed to climatic warming (Burton, 2003), and anecdotal evidence suggests populations in south-east England declined around the 1950s (Bees, Wasps & Ants Recording Society, 2019). Whilst population sizes of *V. vulgaris* fluctuate markedly from year to year, including periods of sustained population increase (Lester *et al.*, 2017), the distribution of this species is believed to have changed little in England (Edwards & Telfer, 2002). *Vespula germanica* has similar population dynamics in England, although this species is thought to have declined in the 1970s and 1980s (Archer 2001, 2018). Long-term understanding of these species' occupancy is important for maintaining ecosystem services and for predicting how anthropogenic change will affect populations of these apex predators. This is especially important given the success of social wasps as invasive species in parts of the world: *V. germanica* and *V. vulgaris* have been highly successful colonisers of South America, New Zealand and Australia where they are causing ecological and economic damage (Lester & Beggs, 2019).

Here, we estimate occupancy trends for three Vespinae species in England from 1900 to 2016 and compare multiple Bayesian occupancy models based on an integrated BWARS-NHM dataset with several combinations of spatial resolution (1 × 1 km, 2 × 2 km, 5 × 5 km or 10 × 10 km grid cells) and temporal resolution (1 year, 5 years or 10 years). Note that we are interested in trends rather than absolute occupancy estimates. To compare models, we quantify how the trends, precision and measures of model fit are affected by varying the closure period-length and spatial grain. We aim to (i) test whether occupancy trends of *Vespula vulgaris*, *Vespula germanica* and *Vespa crabro* have changed in England between 1900 and 2016 and (ii) test the effect of varying spatial and temporal resolutions on model performance when the data are very sparse, such as specimen records. Our general hypothesis is that coarser

resolutions will contain less information but allow model parameters to be estimated more precisely. Our hypotheses for the Vespinae trends are based on previous work demonstrating that ranges (occupancy) of *V. vulgaris* and *V. germanica* have both changed relatively little in England (Archer, 2001, 2018; Edwards & Telfer, 2002), and that *V. crabro* occupancy decreased in the 1950s and increased since 1970 (Bees, Wasps & Ants Recording Society, 2019).

## Materials and methods

### Data collation and standardisation

We digitised all UK *V. vulgaris*, *V. germanica* and *V. crabro* specimens held by the NHM, totalling 1830 specimens collected between 1884 and 2016. Digitisation involved recording all information on specimen labels including collection date and location to the most detailed level available, as well as georeferencing by assigning point coordinates to all collection locations and estimating associated error radii (for protocol, see Blagoderov *et al.*, 2017). We assigned all point coordinates to 1 × 1 km grid cells and removed records with location error radii greater than 10 km. The identifications of NHM Vespinae specimens were recently verified by M. Archer and GRB.

BWARS granted the use of their *V. vulgaris*, *V. germanica* and *V. crabro* records for these analyses, totalling 10 744 records from between 1840 and 2016. These records are UK species observations that specify the observation date and location as grid cells. All records are subject to validation and verification by experts. We removed any records whose locations were less precise than 1 × 1 km grid cells.

For both NHM and BWARS datasets, we only included records from England that dated from 1900 onwards in analyses because the number of records from other countries and earlier years was felt to be insufficient (Supporting Information Fig. S1.1). We included only those record with precise dates.

To test the effect of varying spatiotemporal resolution on model performance, our starting point was a combined NHM + BWARS dataset with record locations and dates defined to 1 × 1 km and 1-day precision, respectively. We coarsened all locations to three additional spatial resolutions: 2 × 2 km, 5 × 5 km and 10 × 10 km grid cells and assigned all record dates to 1-, 5- and 10-year closure periods. The 1 × 1 km grid cell precision provides the greatest number of spatial replicates, 10 × 10 km grid cell precision increases the number of visits (defined as a unique combination of record date and grid cell throughout) per grid cell:closure period combination, whilst 2 × 2 and 5 × 5 km grid cells represents intermediates between the two. *Vespula* workers normally forage within 400 m of their nest (Akre *et al.*, 1975) and foraging distances of *Vespa* workers is assumed to be less than 1 km (Edwards, 1980; Matsuura & Yamane, 1990); hence, all grid cell resolutions capture a colony's range and the spatial closure assumption is reasonable. A 1-year closure period was chosen as the finest temporal scale of estimates. Closure periods of 5 and 10 years were chosen to increase the number of visits within closure period:grid cell combinations. One year is an appropriate temporal unit for meeting

the assumption of temporal closure, since UK Vespine populations have one generation per year (Spradbery, 1973). However, 5- and 10-year closure periods likely violate this assumption, which can lead to inflated occupancy estimates (Steenweg *et al.*, 2018). As such, only models at temporal resolutions of 1 year meet the closure assumption.

Since the model formulation used in these analyses discards grid cells that were only visited in a single closure period throughout the time series, we removed all records from grid cells that had not been visited in at least two 10-year closure periods. This ensures that all models, including those at finer temporal resolutions, are based on the same visits and allows for the comparison of models at different spatiotemporal scales.

The standardisation process resulted in 566 and 3511 records from NHM and BWARS, respectively (Fig. 2; see Supporting Information Fig. S1.1 for a workflow of the standardisation process and the number of records removed at each stage). Both the percentage of grid cells that were visited two or more times within closure periods, and the number of repeat visits to such sites increased with coarser spatiotemporal resolutions, such that there is a 16-fold and a two-fold increase, respectively, when comparing the finest and the coarsest spatiotemporal resolutions (1 km + 1 year vs. 10 km + 10 years; Supporting Information Table S1.2). The geographical coverage of records is biased towards south-east England, indicating that the result of this study may not be representative for all of England (Fig. 3).

### Model choice

Our occupancy model builds on the work of Outhwaite *et al.* (2018) that enabled the use of sparse data by including a random walk in the state sub-model, allowing information to be shared across closure periods. We use a detection sub-model based on that of Van Strien *et al.* (2013), which estimates separate detection probabilities for three categories of visits as independent realisations of the same underlying state. These authors account for varying sampling effort by categorising visits based on the number of species observed per visit. We modified this approach by dividing the NHM + BWARS dataset into three categories based on data source: (i) BWARS 1 sp. visits, that is, BWARS visits with one observed species; (ii) BWARS 2-3 spp. visits, that is, BWARS visits with two or three observed species; and (iii) NHM visits, that is, all NHM visits regardless of the number of observed species. This classification accounts for potential differences in the recording process between the NHM and BWARS data, and for inconsistent sampling effort among two categories of the BWARS data (see Supporting Information Appendix S2 for details on the model formulation).

### Model fitting and evaluation

We fitted Bayesian occupancy models for every combination of grid cell size (1 × 1 km, 2 × 2 km, 5 × 5 km or 10 × 10 km grid cells) and closure period length (1 year, 5 years or 10 years), totalling 12 models per species (see Table 1 for sample
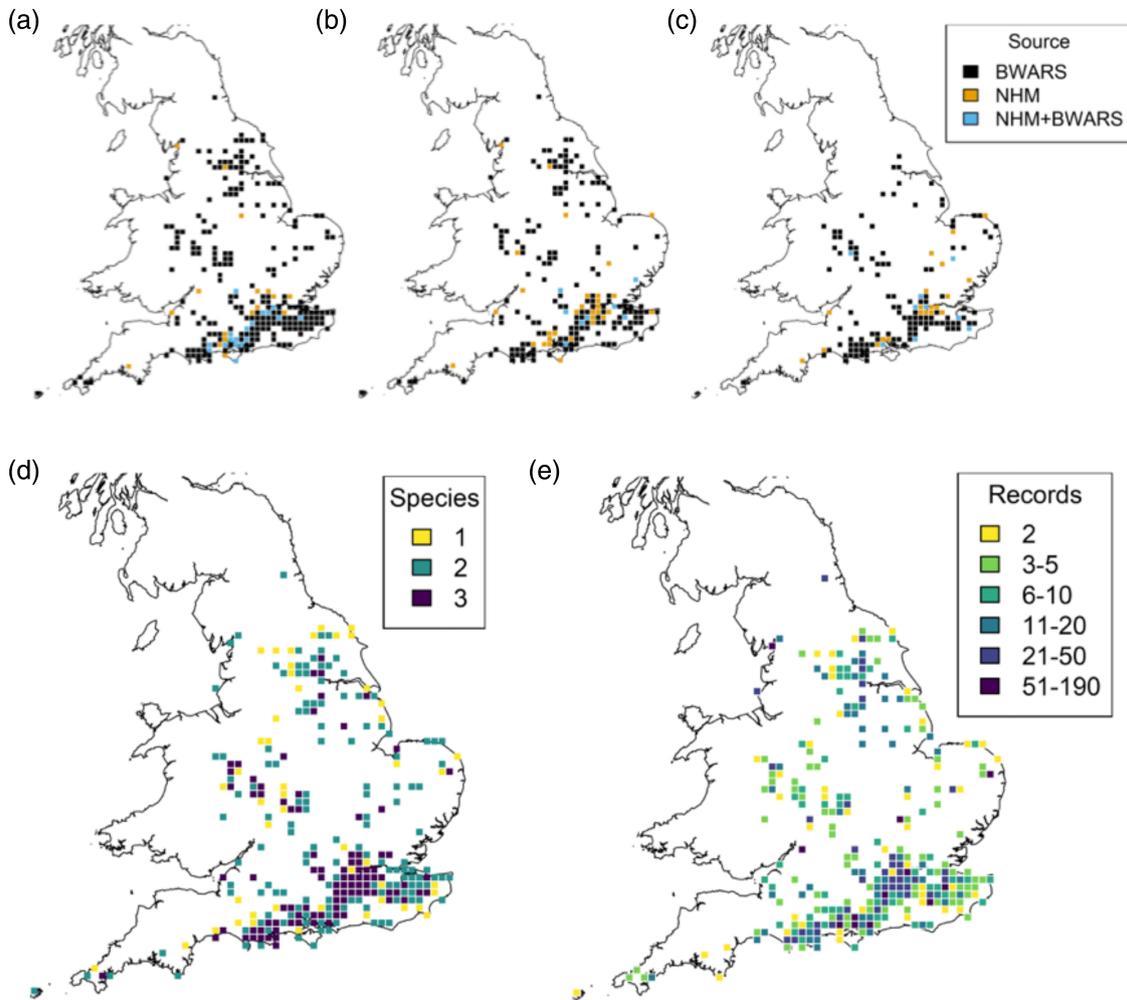
**Figure 3.** The distribution and source of English (a) *Vespula vulgaris*, (b) *Vespula germanica* and (c) *Vespa crabro* records used in analyses. Each square represents a 10 × 10 km grid cell (*n* = 282) coloured according to (d) the total number of species recorded per grid cell between 1900 and 2016, and (e) the total number of records per grid cell between 1900 and 2016 (*n* = 4077). All records are from the Natural History Museum, London (NHM; *n* = 566) or the Bees, Wasps and Ants Recording Society (BWARS; *n* = 3511).

sizes). All models were fitted in a Bayesian mode of inference using JAGS (version 4.3.0; Plummer, 2009) through the R package 'sparta' (version 0.2.06; August *et al.*, 2019) in R (version 3.5.2; R Core Team, 2018) and we selected the random walk model with half-Cauchy hyperpriors. All models were fitted with three Markov chain Monte Carlo chains for 50 000 iterations each with the first 25 000 iterations being discarded as "burn-in". We used the Gelman–Rubin statistic (Rhat; Gelman & Rubin, 1992) to determine convergence of occupancy estimates, where Rhat-values below 1.1 were considered satisfactory (Kéry & Schaub, 2012). The four models estimating *V. germanica* occupancy at the 1-year temporal resolution did not converge and are therefore not presented here.

We used three metrics to evaluate model performance: occupancy trends, detection probability ($\alpha_t$ in Eqn. S2.5) trends and the deviance information criterion (DIC; Spiegelhalter *et al.*, 2002). DIC was chosen over methods that penalise the

deviance by the absolute number of parameters as opposed to the number of effective parameters, since these can suffer from boundary effects (Bolker *et al.*, 2009). As the number of parameters increases with finer spatiotemporal resolutions (Supporting Informatio Fig. S3.2), we also compared deviance and the effective number of parameters, as calculated using the R package 'AICcmodavg' (version 2.2-2; Mazerolle, 2019).

## Results

Varying spatiotemporal resolutions in Bayesian occupancy models showed little effect on trends of occupancy and detection probability for all three species, as evident from overlapping 95% credible intervals (CIs) throughout the time series (Figs. 4 and 5). Similarly, 95% CIs show that spatiotemporal resolution has little effect on the precision of occupancy and detection

**Table 1.** Sample sizes and model specifications including each model's spatial resolution (grid cell size), temporal resolution (closure period length), total number of closure periods, visits and grid cells, in addition to the numbers of grid cells and records for each of *Vespula vulgaris*, *Vespula germanica* and *Vespa crabro*.

| Grid cell size (km) | Closure period length (years) | Total closure periods | Total visits | Total grid cells | Total grid cells per species | | | Total records per species | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | *V. vulgaris* | *V. germanica* | *V. crabro* | *V. vulgaris* | *V. germanica* | *V. crabro* |
| 1 × 1 | 1 | 117 | 3639 | 604 | 497 | NA | 292 | 2053 | NA | 935 |
| 1 × 1 | 5 | 24 | | | | | | | | |
| 1 × 1 | 10 | 12 | | | | | | | | |
| 2 × 2 | 1 | 117 | 3639 | 539 | 447 | 343 | 268 | 2053 | 1089 | 935 |
| 2 × 2 | 5 | 24 | | | | | | | | |
| 2 × 2 | 10 | 12 | | | | | | | | |
| 5 × 5 | 1 | 117 | 3639 | 417 | 358 | 283 | 213 | 2053 | 1089 | 935 |
| 5 × 5 | 5 | 24 | | | | | | | | |
| 5 × 5 | 10 | 12 | | | | | | | | |
| 10 × 10 | 1 | 117 | 3639 | 282 | 256 | 207 | 147 | 2053 | 1089 | 935 |
| 10 × 10 | 5 | 24 | | | | | | | | |
| 10 × 10 | 10 | 12 | | | | | | | | |

probability estimates; however, precision of both estimates increases throughout the time series, particularly after 1970 (Figs. 4 and 5). Longer closure periods tend to smooth out trends and are unable to detect short-term changes in occupancy as well as detection probability (Figs. 4 and 5).

All models show that neither *V. vulgaris*, *V. germanica* nor *V. crabro* have experienced statistically significant changes in occupancy trends when comparing 1900 to 2016 (Fig. 4; Supporting Information Table S3.3). Nonetheless, all models apart from those at a 10 × 10 km spatial resolution show a statistically significant increase in *V. vulgaris* occupancy of 26% (95%CI: 3.2–64%) from 1940 to 1980 when averaged across models (Fig. 4a; Supporting Information Table S3.4). Seven of 12 *V. crabro* models indicate an absolute occupancy increase from 0.29 in 1920 to 0.61 (95%CI: 0.36–0.85) in 1950, when averaged across models (Fig. 4c; Supporting Information Table S3.5). Since 1950, *V. crabro* shows an occupancy decline followed by an increase, which are both statistically significant for all models: the occupancy decreased from 0.61 (95%CI: 0.36–0.85) in 1950 to 0.18 (95%CI: 0.08–0.37) in 1970, and increased to 0.66 (95%CI: 0.45–0.84) in 2016, when averaged across models (Fig. 4c; Supporting Information Table S3.5).

None of the three species showed statistically significant change in detection probability between 1900 and 1990, whilst models at coarse temporal resolutions generally showed decreasing detection probability among *Vespula* species since 1990 (Fig. 5; Supporting Information Table S3.6). Between 1990 and 2016, all models for *V. vulgaris* with closure periods greater than 1 year, and models for *V. germanica* with 10-year closure periods on average showed decreasing detection probabilities of 29.9% (95%CI: 54.6–15.1) and 52.8% (95%CI: 64.2–39.3), respectively (Fig. 5a,b; Supporting Information Table S3.6). No statistically significant change was observed for *V. crabro* between 1990 and 2016 (Fig. 5c; Supporting Information Table S3.6).

For *V. vulgaris* and *V. germanica*, models with coarse spatio-temporal resolutions result in lower DIC-values, whereas for *V. crabro*, finer spatiotemporal resolutions give lower DIC-values (Fig. 6). For all species, finer spatiotemporal resolutions increase the number of effective parameters (Supporting Information Fig. S3.2), whilst decreasing model deviance (Fig. S3.3).

## Discussion

Bayesian occupancy models can yield long-term occupancy trends by integrating sparse presence-only data from natural history collections and species recording schemes. Our findings add to a nascent literature on long-term (>50 year) change in insect biodiversity from museum data (Habel *et al.*, 2019; Soroye *et al.*, 2020; Zattara & Aizen, 2021), although to our knowledge this is the first to present century-long trends at the species level. As evident from the congruence across models, coarsening the spatiotemporal resolution of model estimates has little effect on overall occupancy trends throughout species' time series although information regarding short-term changes are lost. According to DIC-values, the optimal spatiotemporal resolution is species-specific.

We present the first quantitative *V. vulgaris*, *V. germanica* and *V. crabro* trends in England before the 1970s (Fig. 4). Our models suggest that *V. vulgaris* and *V. germanica* trends have remained stable in England from 1900 to 2016, apart from a previously undocumented 26% (95%CI: 3.2–64%) increase in *V. vulgaris* occupancy from 1940 to 1980. This increase was detected in all models at a finer spatial resolution than 10 × 10 km grid cells, further suggesting that coarse spatial resolutions hold less information and tend to smooth out trends. These results provide no support for the suggestion of differential changes in abundance of *V. vulgaris* (stable) and *V. germanica* (declining) in the United Kingdom during the 1970s and 1980s (Archer, 2001). One explanation is that Archer may have observed a decline in local abundance without a loss of range size. On the other hand, *V. crabro* occupancy trends show considerable fluctuations throughout the time series. Two such
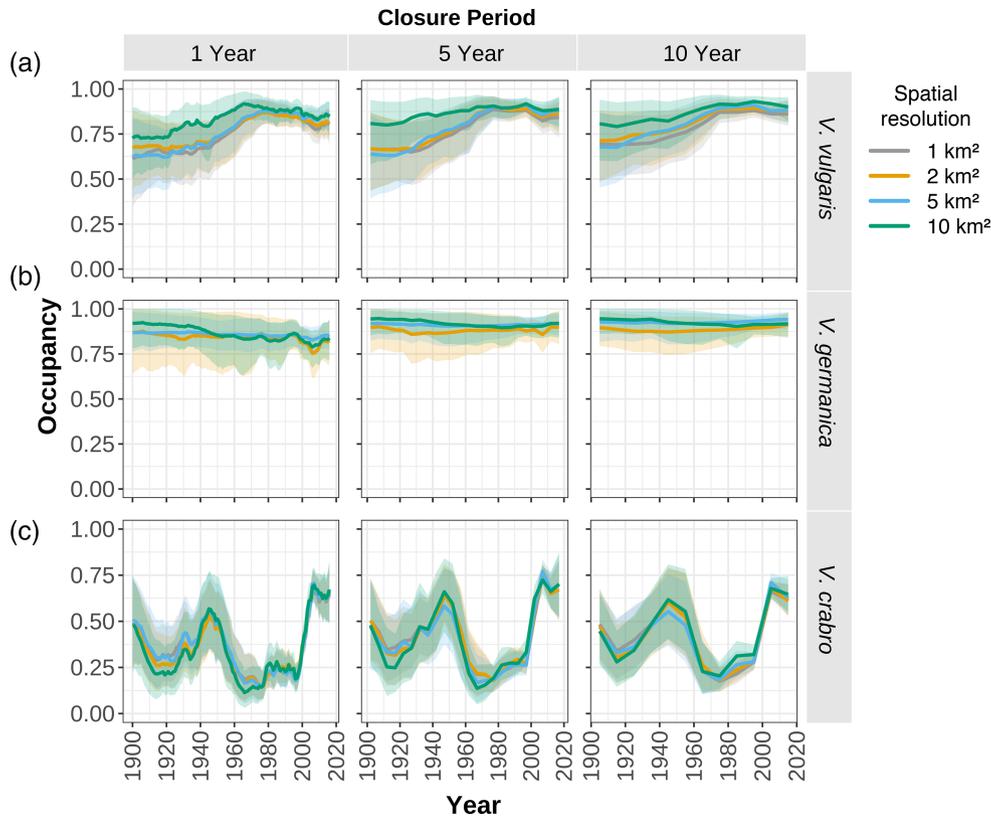
**Figure 4.** Occupancy estimates from Bayesian occupancy models varying in temporal and spatial resolution for each of (a) *Vespula vulgaris*, (b) *Vespula germanica* and (c) *Vespa crabro*. Estimates are for England between 1900 and 2016. The temporal resolutions are closure periods of 1, 5 or 10 years (columns). Model estimates are coloured according to their spatial resolution: 1 × 1 km, 2 × 2 km, 5 × 5 km or 10 × 10 km grid cells. Shaded areas represent 95% credible intervals. See Table 1 for sample sizes.

fluctuations are especially prominent: a decrease from 1950 to 1970, and an increase from 1970 to 2016 (Fig. 4c), which are both in line with previous anecdotal evidence describing the same trend (Bees, Wasps & Ants Recording Society, 2019). At coarse temporal resolutions, *Vespula* species show decreasing detection probabilities since 1990 that is not observed for *V. crabro* (Fig. 5; Supporting Information Table S3.6). This trend is consistent with the hypothesis that naturalists are less likely to record relatively common species, as suggested elsewhere from results of citizen science projects (Isaac & Pocock, 2015), and is worthy of further investigation.

The contrasting patterns between the *Vespa* and *Vespula* occupancy trends may be explained by differences in diet and habitat. A possible explanation for why *V. crabro* declined between 1950 and 1970 whilst *V. vulgaris* and *V. germanica* largely remained stable is that both *V. vulgaris* and *V. germanica* are habitat and dietary generalists (Edwards & Telfer, 2002; Harris, 1991), whereas *V. crabro* is associated with ancient woodlands and farmland, where it nests in mature tree hollows (Edwards, 1997). These land-cover types were disproportionately affected by anthropogenic pressures in the mid-20th century (Peterken & Harding, 1975; Spencer & Kirby, 1992; Robinson & Sutherland, 2002; McKernan & Goldberg, 2011), conceivably causing the observed *V. crabro* decline. An

alternative, but not mutually exclusive, explanation is that *V. crabro* was more severely affected by a series of cold and wet springs between 1950 and 1970 (Mayes & Wheeler, 1997). Since *V. crabro* generally has a more southerly distribution than the two *Vespula* species (Edwards, 1980; Pekkarinen, 1989), it is potentially more negatively affected by cold temperatures; however, these same variables have been identified as having significant effects on *Vespula* populations, with a particular strong negative effect of cold springs on three populations of *V. vulgaris* studied over 39 years (Lester *et al.*, 2017). Extending our approach to more species would permit tests of hypotheses about habitat and diet as factors mediating responses to environmental change over centennial time scales, and allow us to address questions about collection behaviours, e.g., whether the recording of common species is decreasing.

Our models suggest particularly interesting pattern of change for the hornet, *V. crabro*. *Vespa crabro* was largely restricted to southern England when its occupancy plummeted in the mid-20th century (Phillips & Roberts, 2010) and the subsequent increase in occupancy from 1970 returned occupancy to approximately that of the 1950s (Fig. 4c). This period of expansion is believed to be associated with climate warming (Burton, 2003). Supporting this hypothesis, we found a northward shift in the range margin of *V. crabro* during recent decades that is not
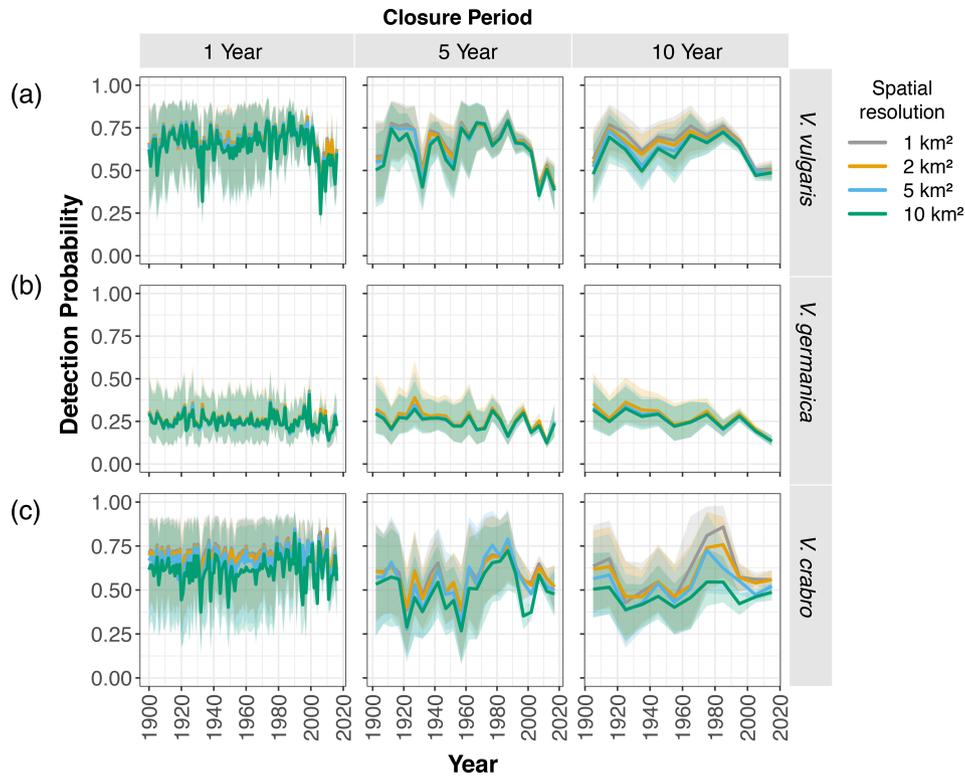
**Figure 5.** Estimates of detection probability, α*ₜ*, from Bayesian occupancy models varying in temporal and spatial resolution for each of (a) *Vespula vulgaris*, (b) *Vespula germanica* and (c) *Vespa crabro*. Estimates are for England between 1900 and 2016. The temporal resolutions are closure periods of 1, 5 or 10 years (columns). Model estimates are coloured according to their spatial resolution: 1 × 1 km, 2 × 2 km, 5 × 5 km or 10 × 10 km grid cells. Shaded areas represent 95% credible intervals. See Table 1 for sample sizes.
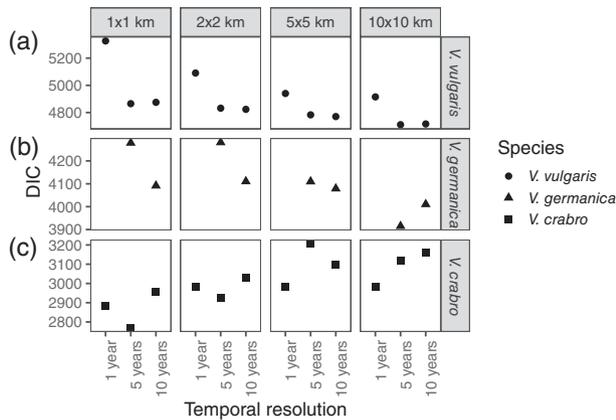


**Figure 6.** DIC-values for multiple Bayesian occupancy models varying in spatiotemporal resolution for each of (a) *Vespula vulgaris* (circles), (b) *Vespula germanica* (triangles) and (c) *Vespa crabro* (squares) in England between 1900 and 2016. The temporal resolutions are closure periods of 1 year, 5 years or 10 years (x-axis). The spatial resolutions are 1 × 1 km, 2 × 2 km, 5 × 5 km or 10 × 10 km grid cells (columns). Note that there are no estimates for *V. germanica* at 1 × 1 km resolutions due to poor convergence. Also note that the y-axes vary among the species. See Table 1 for sample sizes.

matched by *Vespula* species (Supporting Information Fig. S3.4), suggesting that the majority of grid cells colonised during the expansion period were not the same grid cells that were lost during the earlier decades. This result is consistent with the notion that, since 1970, *V. crabro*'s range has been expanding, whilst simultaneously thinning, as reported in some butterfly and moth species (Wilson *et al.*, 2004; Mair *et al.*, 2012; Fox *et al.*, 2014). It is therefore surprising that we observe almost no difference in the occupancy trends of *V. crabro* when measured at different spatial grains (Wilson *et al.*, 2004). These results raise questions that could be addressed using a spatially explicit model of changes in the hornet's distribution during the last century. Northward shifts in range are also expected for *Vespula* populations (Sorvari, 2018). As our analysis was limited to records from England, we are unable to suggest whether there have been occupancy changes at the northern edges of the ranges of *V. germanica* or *V. vulgaris*.

For the three species tested here, we demonstrate that occupancy models can yield fine-grained long-term species-level trends by integrating records from natural history collections and monitoring schemes. Moreover, spatiotemporal resolution has little effect on occupancy trends as well as associated precisions regardless of whether the closure assumption is met.

However, violating the closure assumption by coarsening the temporal resolution, smooths short-term occupancy variation. Our models make contrasting assumptions about the sampling process and employ different strategies for the trade-off between meeting the closure assumption and having sufficient records for estimating detection probability. Hence, the observed congruence across models' occupancy trends serves as an internal validation indicating sufficient power to estimate the detection probability, despite models having up to a 16-fold difference in the percentage of grid cells visited twice or more within closure periods (Supporting Information Table S1.2). Uncertainties with regard to the sampling protocols underlying natural history collections have long been considered a major obstacle to understating long-term species change (Elith *et al.*, 2006; Tingley & Beissinger, 2009; Kissling *et al.*, 2018), but our results demonstrate the potential of detection sub-models to satisfactorily account for such uncertainties. Moreover, as a result of data deficiency, studies estimating long-term species trends from natural history collections often make estimates over aggregated multi-decade periods (e.g., Davidson *et al.*, 2001; Myers *et al.*, 2009; van Strien *et al.*, 2019). We produced long-term trends at the finest spatiotemporal scale tested (1 × 1 km grid cells and 1-year closure period) for two of the three species (*V. germanica* trends showed poor convergence at 1-year closure periods), demonstrating that Bayesian occupancy models can yield fine-grained annual occupancy trends from natural history collections. However, estimates of occupancy and detection probability for all species are more precise after the 1970s, as evident from narrower CIs (Figs. 4 and 5). Since only 15% of the total number of records pre-date 1970, but comprise 60% of the total time series, this result is hardly surprising and further suggests that reasonably precise trends can be obtained from sparse specimen data.

The congruence among models highlights that occupancy trends alone cannot single out an objectively superior spatiotemporal resolution. According to DIC-values, coarse spatiotemporal resolutions are favoured for estimating *V. vulgaris* and *V. germanica* occupancies, whilst the opposite is true for *V. crabro* (Fig. 6). DIC components show the same trend for all three species such that spatiotemporal coarsening decreases the models' number of effective parameters and increases deviance (Supporting Information Figs. S3.2–3). Hence, for species with relatively stable occupancies throughout the time series (i.e. *V. vulgaris* and *V. germanica*), increasing the number of parameters by coarsening the spatiotemporal resolution does not provide additional information to counter the decreased deviance. Conversely, coarsening the spatiotemporal resolution for *V. crabro* occupancy results in a measurable loss of information as evident from these models being least preferred by DIC-values. In contrast with *V. vulgaris* and *V. germanica*, the occupancy of *V. crabro* shows considerable year-to-year variation throughout the time series so additional effective parameters allow interannual variation to be described by models. As a result of additional parameters adding information, the deviance of *V. crabro* models at fine temporal resolutions is penalised to a lesser extent by an increase in the number of effective parameters than for species with stable occupancies.

In order to identify a single superior spatiotemporal resolution for estimating long-term occupancy trends, it is important to differentiate between coarsening spatially versus temporally. According to DIC-values, the optimal spatiotemporal resolution depends on the degree to which occupancy varies throughout species' time series and can therefore only be identified by running multiple models, which can be time-consuming and computationally expensive. We advise against using DIC-values as an objective measure of model fit and instead propose an approach to identify the ideal spatiotemporal resolution that is based on the research question. For answering questions concerning trends over time with sparse data that requires coarsening to estimate model parameters, we suggest that models should maximise the number of closure period parameters by using short closure periods to avoid concealing potential short-term variation. Reducing the number of grid cell parameters by coarsening the spatial resolution does not incur the same cost of concealing short-term variation, although it might overestimate occupancy (Steenweg *et al.*, 2018).

Our results indicate that when very sparse data are used to estimate long-term trends, coarsening the spatial grain is a promising method for achieving sufficient records to estimate parameters in Bayesian occupancy models. However, the model formulation used here assumes that relative detection probabilities, and in effect the record collection processes, are constant among the three data type categories throughout the time series. As previous work indicates that record collection processes may differ between natural history collections and species monitoring schemes (Boakes *et al.*, 2010; Speed *et al.*, 2018), testing these assumptions is a priority for future research.

Our results show that Bayesian occupancy models can yield long-term species trends by spatiotemporally coarsening very sparse data, regardless of whether the closure assumption is met. However, a trade-off exists where coarsening the temporal resolution risks losing information about short-term interannual variation. We argue that one should not blindly follow DIC-values and propose that the most appropriate spatiotemporal resolution will depend on the question asked and data available. Very sparse data should preferentially be spatially coarsened when estimating long-term species trends. The current dearth of such long-term trends is considered a main cause of the observed gradual shift in the accepted norm of the state of biodiversity. This phenomenon, termed shifting baseline syndrome (Pauly, 1995), is considered a major obstacle to conserving biodiversity (Papworth *et al.*, 2009; Soga & Gaston, 2018). For example, our results imply that climate change and large-scale land-use change do not need to be invoked as drivers of change in *V. vulgaris* and *V. germanica* population trends, which contrasts with previous studies (Archer, 2001, 2018; Lester *et al.*, 2017; Bees Wasps & Ants Recording Society, 2019), whilst both drivers seemingly affect *V. crabro* occupancy trends. Given that these drivers are expected to intensify in the future, understanding their separate and interacting effects on social wasps is crucial for maintaining the ecosystem services they provide. Moreover, expanding populations may come with economic and social costs if species become invasive, as evident from expansive, high-density *Vespula* populations in New Zealand (Lester & Beggs, 2019). Hence, the effective control of invasive species also requires understanding of drivers of change, ideally on a national or global scale,

which in turn calls for appropriate statistical integration of multiple datasets such as specimen data and citizen science data presented here. With the increasing availability of presence-only records (including digitised natural history collection specimen records; Graham *et al.*, 2004; Page *et al.*, 2015) from international databases such as the Global Biodiversity Information Facility (GBIF; Troudet *et al.*, 2017), the Bayesian occupancy model formulation used here has the potential to provide novel insights into the numerous species and time periods that were previously considered data deficient.

## ACKNOWLEDGEMENTS

### Data availability statement

All scripts used to generate the analyses presented in this paper are available via https://github.com/galinajonsson/HistoricalWaspOccupancies. The georeferenced Natural History Museum specimen data used in analyses is available via https://doi.org/10.5519/0082541. The model outputs are available via https://doi.org/10.5519/0055095. The Bees, Wasps and Ants Recording Society (BWARS) data is available on request from the National Biodiversity Network (NBN), whose contact details are: The National Biodiversity Network Unit F, 14-18 St. Mary's Gate Lace Market Nottingham, UK Telephone: +44 (0)115 850 0177 Email: support@nbn.org.uk

### Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Appendix S1:** Supporting information
**Appendix S2:** Supporting information
**Appendix S3:** Supporting information

## REFERENCES

Akre, R.D., Hill, W.B., Donald, J.F.M. & Garnett, W.B. (1975) Foraging distances of *Vespula pensylvanica* workers (Hymenoptera: Vespidae). *Journal of the Kansas Entomological Society*, **48**, 12–16.

Archer, M.E. (1985) Population Dynamics of the Social Wasps *Vespula vulgaris* and *Vespula germanica* in England. *The Journal of Animal Ecology*, **54**, 473–485.

Archer, M.E. (2001) Changes in abundance of *Vespula germanica* and *V. vulgaris* in England. *Ecological Entomology*, **26**, 1–7.

Archer, M.E. (2015) Population dynamics of a suburban garden's social wasps (Hymenoptera: Vespidae) over 30 years in Leicester, England. *Entomologist's Monthly Magazine*, **151**, 189–195.

Archer, M.E. (2018) The social wasp *Vespula germanica* (Fabricius) (Hymenoptera: Vespidae) population dynamics in England over 39 years. *Entomologist's Monthly Magazine*, **154**, 149–155.

Atkinson, S. & Townsend, M. (2011) *The State of the UK's Forests, Woods and Trees – Perspectives From the Sector*. The Woodland Trust, Lincolnshire, UK.

August, T.A., Powney, G.D., Outhwaite, C.L., Harrower, C.A., Hill, M., Hatfield, J., Mancini, F.I., Nick J.B. (2019) sparta: Trend Analysis for Unstructured Data. Version 0.2.06. <https://github.com/BiologicalRecordsCentre/sparta>. Accessed 27 Jan 2020.

Bees Wasps & Ants Recording Society (2019) *Vespa crabro*. <https://www.bwars.com/wasp/vespidae/vespinae/vespa-crabro> 1st November 2019

Blagoderov, V., Penn, M., Sadka, M., Hine, A., Brooks, S.J., Siebert, D., Sleep, C., Cafferty, S., Cane, E., Martin, G., Toloni, F., Wing, P., Chainey, J., Duffell, L., Huxley, R., Ledger, S., McLaughlin, C., Mazzetta, G., Perera, J., Crowther, R., Douglas, L., Durant, J., Honey, M., Huertas, B., Howard, T., Carter, V., Albuquerque, S., Paterson, G. & Kitching, I. (2017) iCollections methodology: workflow, results and lessons learned. *Biodiversity Data Journal*, **5**, e19893.

Boakes, E.H., McGowan, P.J.K.K., Fuller, R.A., Chang-qing, D., Clark, N.E., O'Connor, K., & Mace, G.M. (2010) Distorted views of biodiversity: spatial and temporal bias in species occurrence data. *PLoS Biology*, **8**, e1000385.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.S.S. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution*, **24**, 127–135.

Brooks, S.J., Self, A., Toloni, F. & Sparks, T.H. (2014) Natural history museum collections provide information on phenological change in British butterflies since the late-nineteenth century. *International Journal of Biometeorology*, **58**, 1749–1758.

Burton, J.F. (2003) The apparent influence of climatic change on recent changes of range by European insects (Lepidoptera, Orthoptera). *Processings 13th International Colloquium European Invertebrate Survey*, pp. p. 13–21.Leiden, Neatherlands.

Cardoso, P., Branco, V.V., Chichorro, F., Fukushima, C.S. & Macías-Hernández, N. (2019) Can we really predict a catastrophic worldwide decline of entomofauna and its drivers? *Global Ecology and Conservation*, **20**, 4–5.

Carreck, N.L. & Williams, I.H. (2002) Food for insect pollinators on farmland: insect visits to flowers of annual seed mixtures. *Journal of Insect Conservation*, **6**, 13–23.

Conrad, K.F., Warren, M.S., Fox, R., Parsons, M.S. & Woiwod, I.P. (2006) Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biological Conservation*, **132**, 279–291.

Cruickshank, S.S., Ozgul, A., Zumbach, S. & Schmidt, B.R. (2016) Quantifying population declines based on presence-only records for red-list assessments. *Conservation Biology*, **30**, 1112–1121.

Dallimer, M., Tinch, D., Acs, S., Hanley, N., Southall, H.R., Gaston, K.J. & Armsworth, P.R. (2009) 100years of change: Examining agricultural trends, habitat change and stakeholder perceptions through the 20th century. *Journal of Applied Ecology*, **46**, 334–343.

Davidson, C., Shaffer, H.B. & Jennings, M.R. (2001) Declines of the California red-legged frog: Climate, UV-B, habitat, and pesticides hypotheses. *Ecological Applications*, **11**, 464–479.

Edwards, R. (1980) *Social Wasps: Their biology and control*. Rentokil Ltd., Sussex, UK.

Edwards, R. (1997) *Provisional Atlas for the Aculeate Hymenoptera of Britain and Ireland. Part 1*. Bees, Wasps and Ants Recording Society & Biological Records Centre, Huntingdon, UK.

Edwards, R. & Telfer, M.G. (2002) *Provisional Atlas for the Aculeate Hymenoptera of Britain and Ireland. Part 4*. Biological Records Centre, Huntingdon, UK.

Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A:, Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M.M., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S., Wisz, M.S. & Zimmermann, N.E. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129–151.

Fox, R., Oliver, T.H., Harrower, C.A., Parsons, M.S., Thomas, C.D. & Roy, D.B. (2014) Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes. *Journal of Applied Ecology*, **51**, 949–957.

Franzén, M. & Johannesson, M. (2007) Predicting extinction risk of butterflies and moths (Macrolepidoptera) from distribution patterns and species characteristics. *Journal of Insect Conservation*, **11**, 367–390.

Gelman, A. & Rubin, D.B. (1992) Inference from iterative simulation using multiple sequences. *Statistical Science*, **7**, 457–472.

Goulson, D. (2019) The insect apocalypse, and why it matters. *Current Biology*, **29**, R967–R971.

Goulson, D., Lye, G.C. & Darvill, B. (2008) Decline and conservation of bumble bees. *Annual Review of Entomology*, **53**, 191–208.

Graham, C.H., Ferrier, S., Huettman, F., Moritz, C. & Peterson, A.T. (2004) New developments in museum-based informatics and applications in biodiversity analysis. *Trends in Ecology & Evolution*, **19**, 497–503.

Habel, J.C., Trusch, R., Schmitt, T., Ochse, M. & Ulrich, W. (2019) Long-term large-scale decline in relative abundances of butterfly and burnet moth species across south-western Germany. *Scientific Reports*, **9**, 14921.

Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D. & de Kroon, H. (2017) More than 75 percent decline over 27years in total flying insect biomass in protected areas. *PLOS ONE*, **12**, e0185809.

Hambler, C. & Henderson, P.A. (2019) Challenges in Measuring Global Insect Decline. *SSRN Electronic Journal*, http://dx.doi.org/10.2139/ssrn.3347055.

Harmon, J.P., Stephens, E. & Losey, J. (2007) The decline of native coccinellids (Coleoptera: Coccinellidae) in the United States and Canada. *Journal of Insect Conservation*, **11**, 85–94.

Harris, R.J. (1991) Diet of the wasps *vespula vulgaris* and *V. Germanica* in honeydew beech forest of the south Island, New Zealand. *New Zealand Journal of Zoology*, **18**, 159–169.

Heessen, H. (1996) Long-term trends in ten non-target North Sea fish species. *ICES Journal of Marine Science*, **53**, 1063–1078.

Isaac, N.J.B. & Pocock, M.J.O. (2015) Bias and information in biological records. *Biological Journal of the Linnean Society*, **115**, 522–531.

Isaac, N.J.B., van Strien, A.J., August, T.A., de Zeeuw, M.P. & Roy, D.B. (2014) Statistics for citizen science: extracting signals of change from noisy ecological data. *Methods in Ecology and Evolution*, **5**, 1052–1060.

Jetz, W., McPherson, J.M. & Guralnick, R.P. (2012) Integrating biodiversity distribution knowledge: toward a global map of life. *Trends in Ecology and Evolution*, **27**, 151–159.

Jules, E.S. (1996) Yellow Jackets (*Vespula vulgaris*) as a Second Seed Disperser for the Myrmecochorous Plant, *Trillium ovatum*. *American Midland Naturalist*, **135**, 367–369.

Kéry, M. & Schaub, M. (2012) *Bayesian Population Analysis Using WinBUGS: A Hierarchical Perspective*. Elsevier, Oxford, UK.

Kissling, W.D., Ahumada, J.A., Bowser, A., Fernandez, M., Fernández, N., García, E.A., Guralnick, R.P., Isaac, N.J.B., Kelling, S., Los, W., McRae, L., Mihoub, J.B., Obst, M., Santamaria, M., Skidmore, A.K., Williams, K.J., Agosti, D., Amariles, D., Arvanitidis, C., Bastin, L., De Leo, F., Egloff, W., Elith, J., Hobern, D., Martin, D., Pereira, H.M., Pesole, G., Peterseil, J., Saarenmaa, H., Schigel, D., Schmeller, D.S., Segata, N., Turak, E., Uhlir, P.F., Wee, B. & Hardisty, A.R. (2018) Building essential biodiversity variables (EBVs) of species distribution and abundance at a global scale. *Biological Reviews*, **93**, 600–625.

Klapwijk, M.J., Csóka, G., Hirka, A. & Björkman, C. (2013) Forest insects and climate change: long-term trends in herbivore damage. *Ecology and Evolution*, **3**, 4183–4196.

van Klink, R., Bowler, D.E., Gongalsky, K.B., Swengel, A.B., Gentile, A. & Chase, J.M. (2020) Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science*, **368**, 417–420.

Lester, P.J. & Beggs, J.R. (2019) Invasion success and management strategies for social *Vespula* wasps. *Annual Review of Entomology*, **64**, 51–71.

Lester, P.J., Haywood, J., Archer, M.E. & Shortall, C.R. (2017) The long-term population dynamics of common wasps in their native and invaded range. *Journal of Animal Ecology*, **86**, 337–347.

Loft, P., Zayed, Y., Bolton, P. & Baker, C. (2019) *Agriculture: Historical Statistics*. (Briefing Paper No. 03339). London, UK. House of Commons Library. https://commonslibrary.parliament.uk/research-briefings/sn03339/.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, A. A. & Langtimm, C.A. (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, **83**, 2248–2255.

Mair, L., Thomas, C.D., Anderson, B.J., Fox, R., Botham, M.S. & Hill, J. K. (2012) Temporal variation in responses of species to four decades of climate warming. *Global Change Biology*, **18**, 2439–2447.

Matsuura, M. & Yamane, S. (1990) *Biology of the Vespine Wasps*. Springer Verlag, Berlin, Germany.

Mayes, J. & Wheeler, D. (1997) *Regional Climate of the British Isles*. Routledge, Abingdon, UK.

Mazerolle, M.J. (2019) AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). Version 2.2-2. <https://cran.r-project.org/package=AICcmodavg>. Accessed 27 Jan 2020.

McKernan, P. & Goldberg, E. (2011) A review of the revision of the Ancient Woodland Inventory in the South East. Natural England Research Reports Number 042, Peterborough, UK.

Myers, P., Lundrigan, B.L., Hoffman, S.M.G., Haraminac, A.P. & Seto, S.H. (2009) Climate-induced changes in the small mammal communities of the Northern Great Lakes Region. *Global Change Biology*, **15**, 1434–1454.

Ollerton, J., Erenler, H., Edwards, M. & Crockett, R. (2014) Extinctions of aculeate pollinators in Britain and the role of large-scale agricultural changes. *Science*, **346**, 1360–1362.

Outhwaite, C.L., Chandler, R.E., Powney, G.D., Collen, B., Gregory, R. D. & Isaac, N.J.B. (2018) Prior specification in Bayesian occupancy modelling improves analysis of species occurrence data. *Ecological Indicators*, **93**, 333–343.

Outhwaite, C.L., Powney, G.D., August, T.A. & Isaac, N.J.B. (2015) UK Biodiversity Indicators 2015. Indicator C4b. Status of UK priority species: Distribution. Technical background report. DEFRA.

Page, L.M., MacFadden, B.J., Fortes, J.A., Soltis, P.S. & Riccardi, G. (2015) Digitization of biodiversity collections reveals biggest data on biodiversity. *BioScience*, **65**, 841–842.

Papworth, S.K., Rist, J., Coad, L. & Milner-Gulland, E.J. (2009) Evidence for shifting baseline syndrome in conservation. *Conservation Letters*, **2**, 93–100.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.

Carter V., Chainey J., Crowther R., Douglas L., Durant J., Duffell L., Hine A., Honey M., Huertas B., Howard T., Huxley R., Kitching I., Ledger S., McLaughlin C., Martin G., Mazzetta G., Penn M., Perera J., Sadka M., Scialabba E., Self A., Siebert D., Sleep C., Toloni F., & Wing P. (2016) iCollections – Digitising the British and Irish Butterflies in the Natural History Museum, London. *Biodiversity Data Journal*, **4**, e9559.

Pauly, D. (1995) Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology & Evolution*, **10**, 430.

Pekkarinen, A. (1989) The hornet (*Vespa crabro* L.) in Finland and its changing northern limit in northwestern Europe. *Entomologisk Tidskrift*, **110**, 161–164.

Peterken, G.F. & Harding, P.T. (1975) Woodland conservation in eastern England: comparing the effects of changes in three study areas since 1946. *Biological Conservation*, **8**, 279–298.

Phillips, A. & Roberts, S.P.M. (2010) Information Sheet 8: Hornet (*Vespa crabro*). BWARS/Hymettus <https://bwars.com/sites/www.bwars.com/files/info_sheets/Vespa-crabro-info-sheet.pdf> 29th June 2020

Plummer, M. (2009) JAGS. Version 4.3.0. <http://sourceforge.net/projects/mcmc-jags/files/>. Accessed 27 Jan 2020

Pocock, M.J.O., Roy, H.E., Preston, C.D. & Roy, D.B. (2015) The Biological Records Centre: a pioneer of citizen science. *Biological Journal of the Linnean Society*, **115**, 475–493.

Pocock, M.J.O., Tweddle, J.C., Savage, J., Robinson, L.D. & Roy, H.E. (2017) The diversity and evolution of ecological and environmental citizen science. *PLoS One*, **12**, 1–17.

Powney, G.D., Carvell, C., Edwards, M., Morris, R.K.A., Roy, H.E., Woodcock, B.A. *et al.* (2019) Widespread losses of pollinating insects in Britain. *Nature Communications*, **10**, 1018.

R Core Team (2018) *R: A Language and Environment for Statistical Computing. Version 3.5.2*. R Foundation for Statistical Computing, Vienna, Austria <https://www.r-project.org/>.

Richter, M.R. (2000) Social wWasp (Hymenoptera: Vespidae) foraging behavior. *Annual Review of Entomology*, **45**, 121–150.

Robinson, R.A. & Sutherland, W.J. (2002) Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology*, **39**, 157–176.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–60.

Royle, J.A. & Kéry, M. (2007) A Bayesian state-space formulation of dynamic occupancy models. *Ecology*, **88**, 1813–1823.

Sánchez-Bayo, F. & Wyckhuys, K.A.G. (2019) Worldwide decline of the entomofauna: a review of its drivers. *Biological Conservation*, **232**, 8–27.

Saunders, M.E., Janes, J.K. & O'Hanlon, J.C. (2020) Moving on from the insect apocalypse narrative: engaging with evidence-based insect conservation. *BioScience*, **70**, 80–89.

Shortall, C.R., Moore, A., Smith, E., Hall, M.J., Woiwod, I.P. & Harrington, R. (2009) Long-term changes in the abundance of flying insects. *Insect Conservation and Diversity*, **2**, 251–260.

Soberón, J. & Peterson, A.T. (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics*, **2**, 1–10.

Soga, M. & Gaston, K.J. (2018) Shifting baseline syndrome: causes, consequences, and implications. *Frontiers in Ecology and the Environment*, **16**, 222–230.

Sorvari, J. (2018) Habitat preferences and spring temperature-related abundance of German wasp *Vespula germanica* in its nortern range. *Insect Conservation and Diversity*, **11**, 363–369.

Soroye, P., Newbold, T. & Kerr, J. (2020) Climate change contributes to widespread declines among bumble bees across continents. *Science*, **367**, 685–688.

Southon, R.J., Fernandes, O.A., Nascimento, F.S. & Sumner, S. (2019) Social wasps are effective biocontrol agents of key lepidopteran crop pests. *Proceedings of the Royal Society B: Biological Sciences*, **286**, 20191676.

Speed, J.D.M., Bendiksby, M., Finstad, A.G., Hassel, K., Kolstad, A. L. & Prestø, T. (2018) Contrasting spatial, temporal and environmental patterns in observation and specimen based species occurrence data. *PLoS One*, **13**, e0196417.

Spencer, J.W. & Kirby, K.J. (1992) An inventory of ancient woodland for England and Wales. *Biological Conservation*, **62**, 77–93.

Spiegelhalter, D.J., Best, N.G., Carlin, B.P. & van der Linde, A. (2002) Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, **64**, 583–639.

Spradbery, J.P. (1973) *Wasps – An Account of the Biology and Natural History of Social and Solitary Wasps*. Sidgwick and Jackson, London, UK.

Steenweg, R., Hebblewhite, M., Whittington, J., Lukacs, P. & McKelvey, K. (2018) Sampling scales define occupancy and underlying occupancy-abundance relationships in animals. *Ecology*, **99**, 172–183.

van Strien A.J., Meyling A.W.G., Herder J.E., Hollander H., Kalkman V. J., Poot M.J.M., Turnhout S., van der Hoorn B., van Strien-van Liempt W.T.F.H., van Swaay C.A.M., van Turnhout C.A.M., Verweij R.J.T., & Oerlemans N.J. (2016) Modest recovery of biodiversity in a western European country: The Living Planet Index for the Netherlands. *Biological Conservation*, **200**, 44–50.

van Strien, A.J., van Swaay, C.A.M., van Strien-van Liempt, W.T.F.H., Poot, M.J.M. & WallisDeVries, M.F. (2019) Over a century of data reveal more than 80% decline in butterflies in The Netherlands. *Biological Conservation*, **234**, 116–122.

van Strien, A.J., van Swaay, C.A.M. & Termaat, T. (2013) Opportunistic citizen science data of animal species produce reliable estimates of distribution trends if analysed with occupancy models. *Journal of Applied Ecology*, **50**, 1450–1458.

Sumner, S., Law, G. & Cini, A. (2018) Why we love bees and hate wasps. *Ecological Entomology*, **43**, 836–845.

Termaat T., van Strien A.J., van Grunsven R.H.A., De Knijf G., Bjelke U., Burbach K., Conze K.-J., Goffart P., Hepper D., Kalkman V., Motte G., Prins M.D., Prunier F., Sparrow D., van den Top G.G., Vanappelghem C., Winterholler M., & WallisDeVries M.F. (2019) Distribution trends of European dragonflies under climate change. *Diversity and Distributions*, **25**, 936–950.

Thomas, C.D., Jones, T.H. & Hartley, S.E. (2019) "Insectageddon": a call for more robust data and rigorous analyses. *Global Change Biology*, **25**, 1891–1892.

Tingley, M.W. & Beissinger, S.R. (2009) Detecting range shifts from historical species occurrences: new perspectives on old data. *Trends in Ecology & Evolution*, **24**, 625–633.

Troia, M.J. & McManamay, R.A. (2016) Filling in the GAPS: evaluating completeness and coverage of open-access biodiversity databases in the United States. *Ecology and Evolution*, **6**, 4654–4669.

Troudet, J., Grandcolas, P., Blin, A., Vignes-Lebbe, R. & Legendre, F. (2017) Taxonomic bias in biodiversity data and societal preferences. *Scientific Reports*, **7**, 1–14.

Wagner, D.L. (2020) Insect declines in the anthropocene. *Annual Review of Entomology*, **65**, 457–480.

Wilson, R.J., Thomas, C.D., Fox, R., Roy, D.B. & Kunin, W.E. (2004) Spatial patterns in species distributions reveal biodiversity change. *Nature*, **432**, 393–396.

Winker, K. (2004) Natural history museums in a postbiodiversity era. *BioScience*, **54**, 455–459.

Zattara, E.E. & Aizen, M.A. (2021) Worldwide occurrence records suggest a global decline in bee species richness. *One Earth*, **4**, 114–123.