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Long-term trends in the occupancy of ants revealed through use of multi-sourced datasets

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We combined participatory science data and museum records to understand long-term changes in occupancy for 29 ant species in Denmark over 119 years. Bayesian occupancy modelling indicated change in occupancy for 15 species: five increased, four declined and six showed fluctuating trends. We consider how trends may have been influenced by life-history and habitat changes. Our results build on an emerging picture that biodiversity change in insects is more complex than implied by the simple insect decline narrative.

1. Introduction

There is a pressing need to understand which insect taxa are declining, which are stable, which are increasing and why. Most evidence is from bees, butterflies and dragonflies [1–6]; ants, despite their ubiquity, importance and abundance [7,8], have largely been ignored. The dearth of long-term studies of ants is likely attributable to the cost of acquiring data over large temporal and spatial scales [9]. One solution is to combine data from multiple sources [10–12], including museum collections and participatory science (citizen science) projects [4,12–14].

There are several challenges in dealing with long-term data from multiple sources: differential sampling effort [15], species bias [16,17] and identification errors [18]. Bayesian occupancy models [19] have proven useful in addressing these challenges, e.g. by using contextual information on sampling effort [20–22]. Thus, measuring occupancy trends has become a common way to assess biodiversity changes [23].

Here, we use Bayesian occupancy modelling [19,24] to estimate long-term changes in occupancy of 29 Danish ant species from 1900 to 2019 and consider possible drivers.

2. Material and methods

(a) Data

The combined dataset consisted of seven datasets (table 1) binned into decades (figure 1a) and 10 × 10 km grid cells. We excluded detections of unidentified and non-native species, and those without collection date or geographical coordinates. The combined dataset spanned 119 years (108 sampled years), from 1900 to 2019,
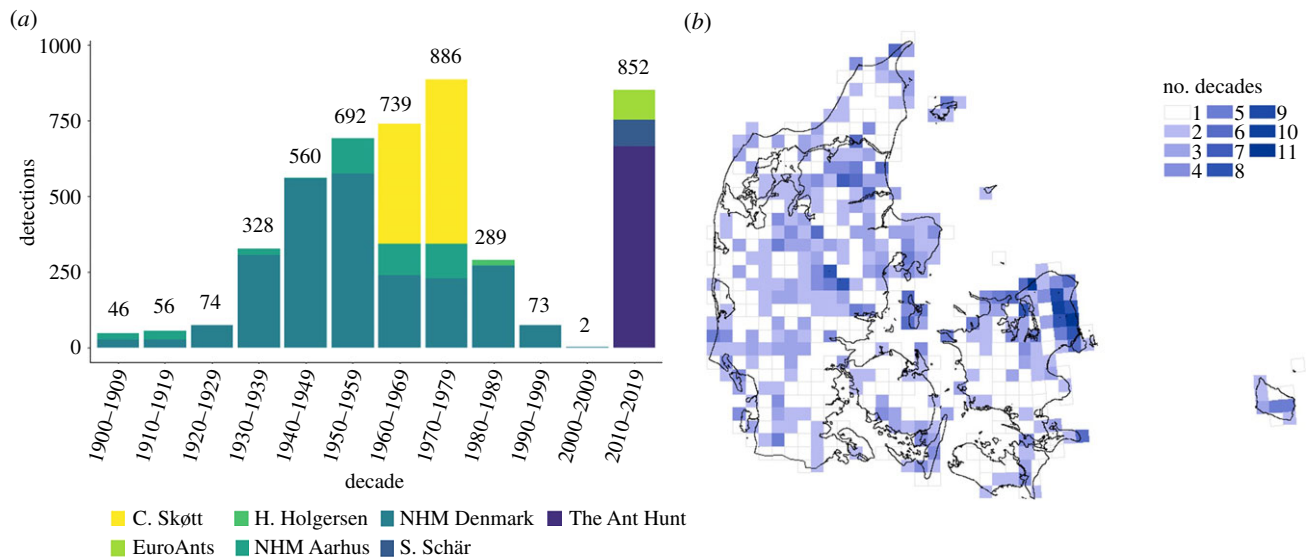
Figure 1. Temporal and spatial distribution of the combined dataset. (*a*) Number of detections for each decade within each dataset. (*b*) Number of decades with data for each 10×10 km grid cell of Denmark.

Table 1. Overview of datasets used in this study after filtering. The combined dataset covered the years 1900–2019; although 12 years were unsampled, all decades were. There were 4597 unique detections for 51 species and 472 10×10 km grid cells, covering 75% of Denmark.

data source	datatype	decades	unique detections	native species	modelled species	total grid cells (included in model)	visits
NHM Denmark[a] [25]	1	11 (1903–2003)	2379	45	29	294 (218)	1552
NHM Aarhus[a] [26]	1	7 (1900–1972)	408	30	24	146 (114)	274
C. Skøtt[b] [27]	1	2 (1960–1979)	940	32	26	216 (166)	885
The Ant Hunt[c] [28]	3	1 (2017–2018)	666	28	23	184 (136)	501
S. Schär[b] [29]	1	1 (2011–2015)	88	29	24	17 (15)	57
EuroAnts[d] [30]	2	1 (2012–2019)	98	27	19	4 (4)	11
H. Holgersen[a] [31]	1	1 (1981–1987)	18	13	13	9 (8)	11
combined		12 (1900–2019)	4597	51	29	472 (284)	3291

[a]Museum collection.
[b]Personal collection.
[c]Participatory science.
[d]Field course.

and included 4597 unique detections (combinations of site, date and species) for 51 species (table 1; electronic supplementary material, S1), covering 75% of Denmark (472 of 633 grid cells; figure 1*b*; electronic supplementary material, S2). However, 188 grid cells were only visited in a single decade. These were excluded from our model, reducing spatial coverage to 45%. Of the remaining 284 grid cells, 88% were included in two or more of the individual datasets.

We classified the data into three data types [12,32], based on information about the sampling protocols and the number of species recorded during a visit (electronic supplementary material, S3). Most datasets are based on collections, which are likely presence-only datasets and were categorized as datatype1. However, EuroAnts is a field course where students record all species found at sites, so was categorized as datatype2. The Ant Hunt used 2 h baiting experiments rather than active searching and was categorized as datatype3. These last two datasets are more likely to contain true absence data. Further information about the datasets is provided in electronic supplementary material, S1–S4.

Species detections were converted to detection histories [33] by organizing data into visits (unique grid cell–date combinations).

Species were assigned a 1 if detected during a visit and a 0 if not, generating non-detections [5,32,34–36]. Species were selected for occupancy modelling based on the total number of detections, proportion of non-detections and the 90th percentile of detections within decades, resulting in 30 species [37,38]. We excluded *Lasius platythorax*, a species only recently separated from *Lasius niger* [39], leaving 29 species (electronic supplementary material, S5).

(b) Bayesian occupancy modelling

We fitted a Bayesian occupancy model for each species following [12,38–41] to estimate occupancy (proportion of occupied 10×10 km grid cells) per decade from 1900 to 2019.

The occupancy model consists of two submodels. The state model describes the true occupancy state of a species (1 or 0) based on the probability of occupancy ψ at a grid cell i during a decade t: $z_{it} \sim \text{Bernoulli}(\psi_{it})$; $\text{logit}(\psi_{it}) = \log(\psi_{it}/1 - \psi_{it}) = b_t + u_i$, where b_t and u_i are the effects of grid cell and decade. Observations (y) are conditional on the species being present ($z = 1$): $y_{itv} | z_{it} \sim \text{Bernoulli}(p_{itv} * z_{it})$, where p is the detection probability and v is a visit. Detection is modelled in the observation submodel. For

each visit (v), grid cell (i) and decade (t), for a given datatype, the probability of detection is given by $\text{logit}(p_{itv}) = \log(p_{itv}/1 - p_{itv}) = a_t + \beta_1 * \text{datatype2}_{itv} + \beta_2 * \text{datatype3}_{itv}$, where a_t is the decade effect. Parameters β_1 and β_2 estimate differences in $\log(p_{itv})$ for datatype2 and datatype3, relative to datatype1.

Model priors were set following others, with vague, uninformative priors for all parameters except the decade effect of the state model, where we use a random walk, allowing the model to share information between time periods, which is especially advantageous for datasets with low recording intensity [38,40,42]:

$$bt \sim \begin{cases} \text{Normal}(\mu_b, 10^4) & \text{for } t = 1 \\ \text{Normal}(b_{t-1}, \sigma_b^2) & \text{for } t > 1 \end{cases}$$

where $\mu_b \sim \text{Normal}(0, 100)$ and $\sigma_b \sim |\text{Student-}t \text{ on 1 d.f.}|$.

Data formatting and Bayesian occupancy modelling were carried out in the package sparta version 0.2.7 in R v. 3.6.3 [41,43] using JAGS v. 4.3.0 [44] through the package R2jags version 0.6.1 [45], with half-Cauchy hyperpriors using three chains, 50 000 iterations, a burn-in of 25 000 iterations and a thinning rate of 3 [35]. If convergence (Rhat < 1.1) [24,46] was not reached, models were rerun doubling the number of iterations and always discarding half as burn-in.

We evaluated model performance by calculating the median uncertainty (the width of the 68% credible interval (1 s.d. either side of the mean)) for each species across decades and for each decade across species. We then calculated Spearman's rank correlation between uncertainty and (i) number of detections for a species, (ii) median occupancy and (iii) decade.

(c) Occupancy change

We calculated the mean occupancy for each decade and identified the peaks and troughs for each species. We calculated the difference between the peaks and troughs and report a 'confidence' score for change as the percentage of the posterior distribution that has the same sign as the mean. Species with confidence scores less than 80% were classified as stable. If confidence scores were greater than or equal to 80%, species with only positive changes were categorized as increasing, species with only negative changes as declining and species that showed both positive and negative changes as fluctuating. We interpret a confidence score greater than or equal to 95% as strong evidence of change, greater than or equal to 90% as moderate evidence, and greater than or equal to 80% as weak evidence.

3. Results

Five species increased in occupancy, four declined, six fluctuated and 14 were stable (figure 2), including some that show change, but with too high uncertainty to draw firm conclusions (electronic supplementary material, S4 and S6). Spearman's rank correlation showed no correlation between uncertainty and the number of detections ($\rho = 0.26$, $p = 0.17$) or decade ($\rho = -0.35$, $p = 0.27$), but there was a significant correlation with species occupancy ($\rho = 0.48$, $p = 0.008$; electronic supplementary material, S7).

(a) Increasing species

Camponotus herculeanus increased from 0.04 in 1900–1909 to 0.09 in 1940–1949 (125% change, 82% confidence). It remained stable until 1950–1959, then increased from 0.065 to 0.24 in 2010–2019 (269% change, 97% confidence). *Formica picea* increased from 0.25 in 1900–1909 to 0.41 in 1970–1979 (64% change, 83% confidence), then stabilized. *Formica rufa* increased from 0.67

in 1900–1909 to 0.84 in 1970–1979 (25% change, 83% confidence), where it stabilized. *Formica uralensis* increased from 0.05 in 1900–1909 to 0.27 in 1970–1979 (440% change, 97% confidence), then stabilized until 1980–1989 (79% confidence) before increasing again from 0.19 to 0.35 in 2010–2019 (84% change, 87% confidence). *Myrmica ruginodis* was stable until 1950–1959, then increased from 0.80 to 0.88 in 1970–1979 (10% change, 83% confidence), where it stabilized.

(b) Declining species

Lasius fuliginosus was stable until 1920–1929, then declined from 0.71 to 0.43 in 1970–1979 (39% change, 94% confidence), where it stabilized. *Myrmica rubra* was stable until 1940–1949, then declined from 0.87 to 0.62 in 1990–1999 (29% change, 88% confidence). *Myrmica sabuleti* was stable until 1940–1949 before declining from 0.70 to 0.05 in 2010–2019 (93% change, 100% confidence). *Myrmica schencki* was stable until 1940–1949, then declined from 0.37 to 0.24 in 2010–2019 (35% change, 82% confidence).
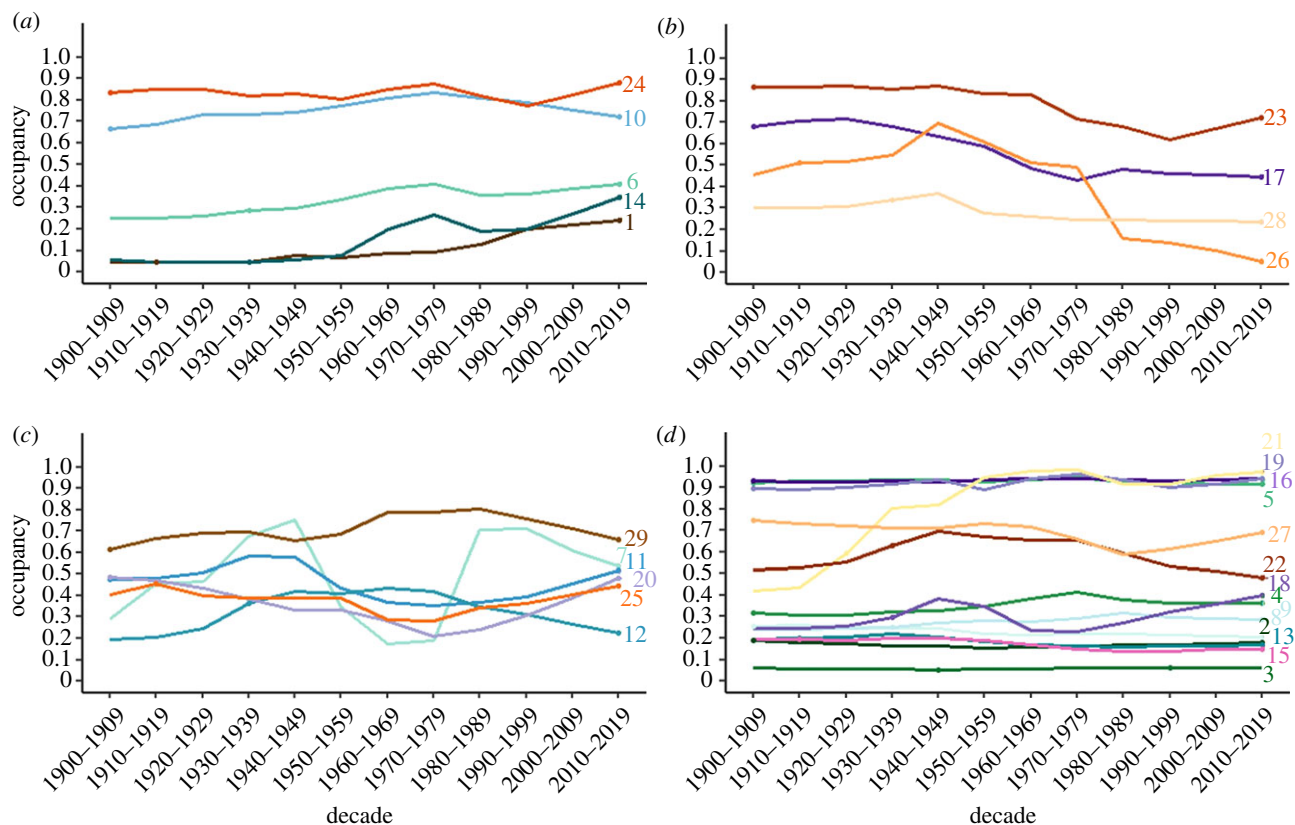
(c) Fluctuating species

Formica polyctena increased from 0.29 in 1900–1909 to 0.75 in 1940–1949 (159% change, 88% confidence), then declined to 0.17 in 1960–1969 (77% change, 99% confidence), and increased to 0.71 in 1990–1999 (318% change, 99% confidence) before declining to 0.54 in 2010–2019 (24% change, 80% confidence). *Formica rufibarbis* was stable until 1930–1939, then declined from 0.58 to 0.35 in 1970–1979 (40% change, 95% confidence). It then increased to 0.52 in 2010–2019 (49% change, 85% confidence). *Formica sanguinea* increased from 0.20 in 1900–1909 to 0.43 in 1960–1969 (115% change, 89% confidence), then declined to 0.22 in 2010–2019 (49% change, 93% confidence). *Lasius umbratus* declined from 0.49 in 1900–1909 to 0.21 in 1970–1979 (57% change, 92% confidence) then increased to 0.48 in 2010–2019 (129% change, 94% confidence). *Myrmica rugulosa* was stable until 1940–1949, then declined from 0.39 to 0.28 in 1970–1979 (28% change, 86% confidence) then increased to 0.44 in 2010–2019 (57% change, 83% confidence). *Tetramorium caespitum* was stable until 1940–1949, then increased from 0.66 in 1940–1949 to 0.80 in 1980–1989 (21% change, 83% confidence), then declined back to 0.66 in 2010–2019 (18% change, 86% confidence).

4. Discussion

Although 14 of 29 species showed stable occupancies from 1900 to 2019, estimates remained imprecise for many species, and 22 species could not be assessed owing to data deficiency (electronic supplementary material, S1 and S5). However, the analysed species exhibit typical behaviours, life histories, foraging strategies, etc. of many native Danish ants.

Four declining species and three fluctuating species exhibit declines in recent years. Two of these (*F. polyctena* and *F. sanguinea*) are mound-building species typically found in forests with open, sun-exposed areas [47,48], along with *Lasius fuliginosus*, which commonly forms large carton nests in cavities at the base of old trees [48]. Danish forests have been increasing since the 1900s and today cover 14.7% of the country [49]. This decline is mainly driven by an increase in monocultures of coniferous plantations [50], which are generally dense and with low light levels in the understorey. Closure of the tree

ID	species	trend	ID	species	trend	ID	species	trend
1	*Camponotus herculeanus*	increasing	11	*Formica rufibarbis*	fluctuating	21	*Leptothorax acervorum*	stable
2	*Formica cinerea*	stable	12	*Formica sanguinea*	fluctuating	22	*Myrmica lobicornis*	stable
3	*Formica cunicularia*	stable	13	*Formica truncorum*	stable	23	*Myrmica rubra*	declining
4	*Formica exsecta*	stable	14	*Formica uralensis*	increasing	24	*Myrmica ruginodis*	increasing
5	*Formica fusca*	stable	15	*Formicoxenus nitidulus*	stable	25	*Myrmica rugulosa*	fluctuating
6	*Formica picea*	increasing	16	*Lasius flavus*	stable	26	*Myrmica sabuleti*	declining
7	*Formica polyctena*	fluctuating	17	*Lasius fuliginosus*	declining	27	*Myrmica scabrinodis*	stable
8	*Formica pratensis*	stable	18	*Lasius meridionalis*	stable	28	*Myrmica schencki*	declining
9	*Formica pressilabris*	stable	19	*Lasius niger*	stable	29	*Tetramorium caespitum*	fluctuating
10	*Formica rufa*	increasing	20	*Lasius umbratus*	fluctuating			

Figure 2. Occupancy trends for 29 ant species in Denmark based on decades from 1900 to 2019. Each line represents a species labelled by a number as indicated in the key. Lines depict the mean of the posterior distribution of occupancy estimates for each decade: the same data are plotted with credible intervals in electronic supplementary material, S4. Points represent the first and last decade where a species has been detected. (*a*) Increasing, (*b*) declining, (*c*) fluctuating and (*d*) stable.

canopy, habitat change and disturbance have caused declines in *Formica* spp. elsewhere [51]. Two forest species (*C. herculeanus* and *F. rufa*) increased in occupancy (though the trend for *F. rufa* may be changing with a 14% decline from 1970–1979 to 2010–2019, 73% confidence). *Camponotus herculeanus* typically occurs in coniferous or mixed conifer–broadleaf forests with a high percentage of *Picea abies* [47,51], which is one of the most common Danish trees [49].

Three of the species that have shown some decline (*M. sabuleti*, *M. schencki*, *T. caespitum*) occur in dry open habitats [47,48]. Their decline may be linked to decreases in available habitat and increases in precipitation. The extent of dry, open habitats in Denmark has declined from approximately 25% in 1888 to less than 10% in 2004, owing to conversion to agriculture and forest [50]. Average precipitation (mm) and days with greater than or equal to 10 mm precipitation have increased from 712 mm and 17 days in 1961–1990 to 791.9 mm and 20.3 days in 2006–2015 [52]. Conversely, three of the recently increasing species (*M. ruginodis*, *F. picea* and *F. uralensis*) occur in wetter habitats, such as bogs and water-drenched soils [48].

Dietary specialists may be more sensitive to disturbance, such as urbanization [53]. Most Danish ants are generalist omnivores, but the diets of four recently declining species (*L. fuliginosus*, *M. schencki*, *F. polyctena* and *F. sanguinea*) tend to be especially protein-rich [48].

Finally, changes in the occupancy of some ant species may be due to changes in conditions for other species on which they depend. In areas where they co-occur, *F. uralensis* is outcompeted by *F. sanguinea* and *M. rubra* [48], so its increase could be linked to decreasing competition. *Lasius umbratus* (currently increasing) depends on species such as *L. niger* and *L. platythorax* for nest construction [48] and may benefit from *L. niger* being the most common ant species in Denmark.

5. Conclusion and future directions

We provide the first insights to our knowledge into long-term occupancy trends for ants. We find declining species are associated with dry, undisturbed habitats and open forests and have protein-rich diets, whereas increasing species are wet- and disturbance-tolerant and tend to be omnivores. These trends appear to be directly linked to changes in habitat and climate.

Ants can host many dependent species [54,55]. As a result, species that depend on declining ant species may also decline.

For example, 70 taxa were found in nests of *F. polyctena* [55] and the decline in the distribution of *M. sabuleti* may be a contributing factor to the decline in its butterfly parasite, *Phengaris* (= *Maculinea*) *arion*, which is currently found in only one area of Denmark [56].

A key caveat of studying ants compared with other insect taxa is that colonies are the units of selection, and colonies can persist for decades, while workers might live for less than a year. However, most of the data come from collections of workers.

The lack of standardized long-term data is problematic for many taxa besides ants, and this challenge is unlikely to change in the near future. While combining multi-sourced data is helpful, and may shed some light on the occupancy of overlooked taxa, it is not a panacea. Many species lack sufficient data for modelling. Participatory science has proven efficient for compiling data, yet participants may overlook rare and cryptic species and are likely to be spatially biased. Combining participatory science with expert searches and focusing on the resampling of sites could prove beneficial. For example, in this study, 188 grids were visited in just one decade. Through resampling, spatial coverage could be increased to 75%, thereby improving our ability to understand both historic and future trends in occupancy.

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