Article (refereed) - postprint

Sheard, Julie K.; Rahbek, Carsten; Dunn, Robert R.; Sanders, Nathan J.; Isaac, Nick J.B. 2021. **Long-term trends in the occupancy of ants revealed through use of multi-sourced datasets.** *Biology Letters*, 17 (10), 20210240. 6, pp. https://doi.org/10.1098/rsbl.2021.0240

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

Running title: Occupancy trends in ants

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ABSTRACT

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 fifteen 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.

Key words: Bayesian occupancy modelling, citizen science, Denmark, Formicidae, museum data.

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 1900-2019 and consider possible drivers.

MATERIAL AND METHODS

(a) Data

The combined data set consisted of seven data sets (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 geographic coordinates. The combined data set spanned 119 years (108 sampled years), from 1900-2019, and included 4,597 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 1b; 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 data sets.

Table 1. Overview of data sets used in this study after filtering. The combined data set covered the years 1900-2019; although 12 years were unsampled, all decades were. There were 4,597 unique detections for 51 species and 472 10 x 10 km grid cells, covering 75 % of Denmark. [1]Museum collection, [2]Personal collection, [3]Participatory science, [4]Field Course.

data source	datatype	decades	unique detections	native species	modelled species	Total grid cells (included in model)	visits
NHM Denmark[1] [25]	1	11 (1903-2003)	2379	45	29	294 (218)	1552
NHM Aarhus[1] [26]	1	7 (1900-1972)	408	30	24	146 (114)	274
C. Skøtt[2] [27]	1	2 (1960-1979)	940	32	26	216 (166)	885
Ant Hunt[3] [28]	3	1 (2017-2018)	666	28	23	184 (136)	501
S. Schär[2] [29]	1	1 (2011-2015)	88	29	24	17 (15)	57
EuroAnts[4] [30]	2	1 (2012-2019)	98	27	19	4 (4)	11
H. Holgersen[1] [31]	1	1 (1981-1987)	18	13	13	9 (8)	11
combined		12 (1900-2019)	4,597	51	29	472 (284)	3,291

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 data sets are based on collections, which are likely presence-only data sets and were categorised as datatype1. However, EuroAnts is a field course where students record all species found at sites, so was categorised as datatype2. The Ant Hunt used two-hour baiting experiments rather than active searching and was categorised as datatype3. These last two data sets are more likely to contain true absence data. Further information about the data sets is provided in electronic supplementary material, S1-S4.

Species detections were converted to detection histories [33] by organising 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 [32,34–37]. Species were selected for occupancy modelling based on total number of detections, proportion of non-detections and the 90th percentile of detections within decades, resulting in 30 species [38,39]. We excluded *Lasius platythorax*, a species only recently seperated from *Lasius niger* [40], leaving 29 species (electronic supplementary material, S5).

(b) Bayesian occupancy modelling

We fitted a Bayesian occupancy model for each species following [12,32,39,41,42] to estimate occupancy (proportion of occupied 10 x 10 km grid cells) per decade from 1900-2019.

The occupancy model consists of two sub models. 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*: $z_{it} \sim$ Bernoulli(ψ_{it}); logit(ψ_{it}) = log(ψ_{it}/1-ψ_{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): $y_{itv}|z_{it} \sim$ Bernoulli($p_{itv}*z_{it}$), where *p* is the detection probability (*p*). Detection is modelled in the observation sub-model. For each visit (*v*), grid cell (*i*) and decade (*t*), for a given datatype the probability of detection is given by 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, relatively 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 data sets with low recording intensity [39,41,42]:

$$bt \sim \begin{cases} Normal(\mu_b, 10^4)\ for\ t=1 \\ Normal(b_{t-1}, \sigma_b^2)\ for\ t>1 \end{cases}, \text{ where, } \mu_b \sim \text{Normal}(0,100) \text{ and } \sigma b \sim |\text{Student-t on 1 df}|$$

Data formatting and Bayesian occupancy modelling were carried out in the package sparta version 0.2.7 in R version 3.6.3 [43,44] using JAGS version 4.3.0 [45] through the package R2jags version 0.6.1 [46], with half-Cauchy hyperpriors using 3 chains, 50,000 iterations, a burn in of 25,000 iterations and a thinning rate of 3 [36]. If convergence (Rhat < 1.1) [24,47] 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 standard deviation 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 1) number of detections for a species, 2) median occupancy and 3) decade.

Occupancy change

We calculated 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 <80 % were classified as stable. If confidence scores were ≥80 %, species with only positive changes were categorised 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 ≥ 95 % as strong evidence of change, ≥ 90 % as moderate evidence, and ≥ 80 % as weak evidence.

RESULTS

Five species increased in occupancy, four declined, six fluctuated, and fourteen 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).

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 stabilised. *Formica rufa* increased from 0.67 in

1900-1909 to 0.84 in 1970-1979 (25 % change, 83 % confidence), where it stabilised. *Formica uralensis* increased from 0.05 in 1900-1909 to 0.27 in 1970-1979 (440 % change, 97 % confidence), then stabilised 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.

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 stabilised. *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).

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).

DISCUSSION

Although 14 of 29 species showed stable occupancies from 1900-2019, 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 [48,49]. Danish forests have been increasing since the 1900s and today cover 14.7 % of the country [50]. This decline is mainly driven by an increase in monocultures of coniferous plantations [51], which are generally dense and with low light levels in the understorey. Closure of the tree canopy, habitat change, and disturbance have caused declines in *Formica* spp. elsewhere [52]. 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* [48,52], which is one of the most common Danish trees [50].

Four of the species that have shown some decline (*L. fuliginosus*, *M. sabuleti*, *M. schencki*, *T. caespitum*) occur in dry open habitats [48,49]. 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 ~ 25 % in 1888 to < 10 % in 2004, owing to conversion to agriculture and forest [51]. Average precipitation (mm) and days with ≥ 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 [53]. 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 [49].

Dietary specialists may be more sensitive to disturbance, such as urbanisation [54]. 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 [49].

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* [49], 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 [49] and may benefit from *L. niger* being the most common ant species in Denmark.

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 [55,56]. As a result, species that depend on declining ant species may also decline. For example, 70 taxa were found in nests of *F. polyctena* [56] and the decline in the distribution of *M. sabuleti* may be a contributing factor to the decline in its butterfly parasite, *Maculinea arion*, which is currently found in only one area of Denmark [57].

A key caveat of studying ants compared to 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 standardised 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 lacked 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 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.

FUNDING

This work was supported by the June 15th Foundation, Knud Højgaards Foundation, the Augustinus Foundation, the Beckett Foundation and the Danish National Research Foundation (DNRF96).

ACKNOWLEDGEMENTS

We would like to thank Anders Tøttrup, Pernille Hjort and Mia Pedersen, who were instrumental in the success of the Ant Hunt. We received support from the Natural History Museum of Denmark, the Danish Nature Agency, Mogens Gissel, the Natural History Museum Aarhus, David Nash, Bjørn Hermansen, and the families and schools who participated in the Ant Hunt.

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FIGURE AND TABLE LEGENDS

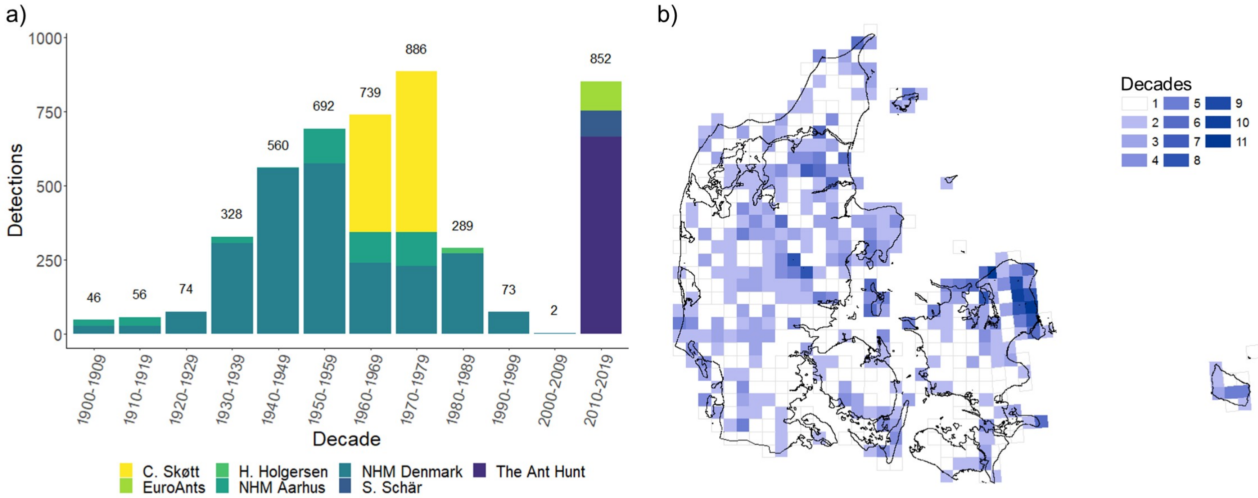
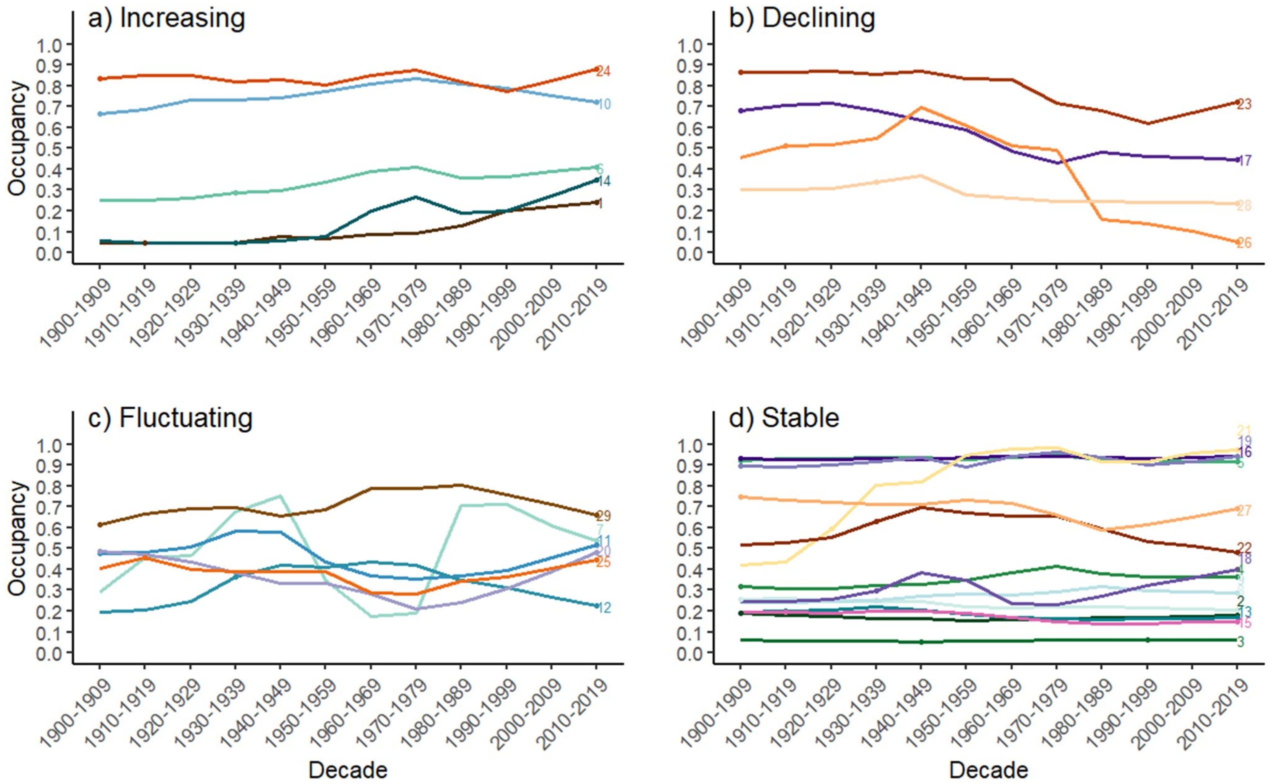


Figure 1. Temporal and spatial distribution of the combined data set. a) Number of detections for each decade within each data set. b) Number of decades with data for each 10 × 10 km grid cell of Denmark.



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

Figure 2. Occupancy trends for 29 ant species in Denmark based on decades from 1900-2019. 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 ESM S4. Points represent the first and last decade where a species has been detected.

Table S1: Overview of all native species found in Denmark, including first and last detection year, number of detections in each dataset and the total number of detections.

species	decades	years			detections							
		first	last	total (n)	Ant Hunt	EuroAnts	Holgersen	NHM Aarhus	NHM Denmark	Schär	Skøtt	total
Camponotus herculeanus	9	1913	2015	30		2		2	36	1	4	45
Camponotus ligniperda	6	1929	2015	9				1	7	1	1	10
Formica cinerea	9	1909	2018	30	6		2		55		9	72
Formica clara	1	2012	2018	2	4	1						5
Formica cunicularia	5	1942	1994	16					22			22
Formica exsecta	8	1908	2017	36	1		1	3	43	2	33	83
Formica foreli	1	2012	2019	3		3				1		4
Formica forsslundi	2	1974	1989	2					2			2
Formica fusca	12	1901	2019	77	85	5	1	37	196	3	84	411
Formica gagatoides	2	1964	1972	3				2	2			4
Formica lugubris	2	1941	2018	2	1				1			2
Formica picea	8	1935	2019	32	1	2	1		28	2	43	77
Formica polyctena	10	1914	2019	52	34	6			109	3		152
Formica pratensis	10	1908	2017	36	1			3	47		16	67
Formica pressilabris	7	1939	2017	32	1	2	1	1	40		13	58
Formica rufa	11	1908	2018	68	7	3		50	154	3	87	304
Formica rufibarbis	10	1909	2019	55	4	5		2	128	4	12	155
Formica sanguinea	8	1935	2018	48	2	2		3	101	1	41	150
Formica truncorum	8	1918	2017	27	2			2	37	1	4	46
Formica uralensis	7	1938	2019	20		3	1	1	48	1	29	83
Formicoxenus nitidulus	7	1912	2012	19				1	21	1	3	26
Harpagoxenus sublaevis	2	1964	1974	6					9		7	16
Hypoponera punctatissima	6	1944	2017	9	1				18		9	28
Lasius brunneus	6	1907	2019	8		1		1	8			10
Lasius flavus	9	1903	2019	48	22	6	1	16	71	4	52	172
Lasius fuliginosus	11	1908	2019	54	11	5	2	14	79	1	21	133
Lasius meridionalis	8	1935	2015	25					36	6		42
Lasius mixtus	7	1913	1971	10					12		2	14

Lasius niger	11	1903	2019	77	323	5	3	37	196	6	90	660
Lasius platythorax	1	2012	2018	5	41	7				4		52
Lasius psammophilus	1	2012	2019	6	2	4				4		10
Lasius umbratus	11	1900	2019	51	1	4		13	60	4	8	90
Leptothorax acervorum	10	1924	2019	42		5		6	84	6	88	189
Leptothorax muscorum	2	1971	1993	4					2		2	4
Myrmecina graminicola	1	1970	1970	1				1				1
Myrmica lobicornis	7	1933	2017	32	2			1	35	1	14	53
Myrmica rubra	11	1902	2019	70	37	4	1	49	158	7	46	302
Myrmica ruginodis	10	1904	2019	66	35	7	1	106	126	4	81	360
Myrmica rugulosa	10	1913	2018	48	6			18	62	4	18	108
Myrmica sabuleti	10	1911	2019	47	4	4		2	93	4	15	122
Myrmica scabrinodis	11	1901	2017	63	4	5	1	26	108	6	39	189
Myrmica schencki	7	1936	2018	28	3			1	39		6	49
Myrmica specioides	3	1941	2012	3		1			2	1		4
Myrmica sulcinodis	5	1936	1973	10				1	12		12	25
Stenamma debile or *S. westwoodii*	2	1958	1995	2				1	1			2
Temnothorax interruptus	3	1969	1980	3					5			5
Temnothorax nylanderi	2	1988	2012	2		1			1			2
Temnothorax parvulus	1	2012	2012	1		1						1
Temnothorax tuberum	3	1942	1985	4					5			5
Tetramorium atratulum	1	1942	1942	1					1			1
Tetramorium caespitum	11	1903	2019	50	25	4	2	7	79	2	51	170

Figure S2: 10x10 km grid cell map of each of the data sets used in the study: a) the Natural History Museum of Denmark, scaled by number of occurrences, b) Christian Skøtt, scaled by number of occurrences, c) Natural History Museum of Aarhus, scaled by number of occurrences, d) Sämi Schär, scaled by number of occurrences, e) the Ant Hunt, scaled by number of occurrences and f) EuroAnts and Holger Holgersen, no scaling.

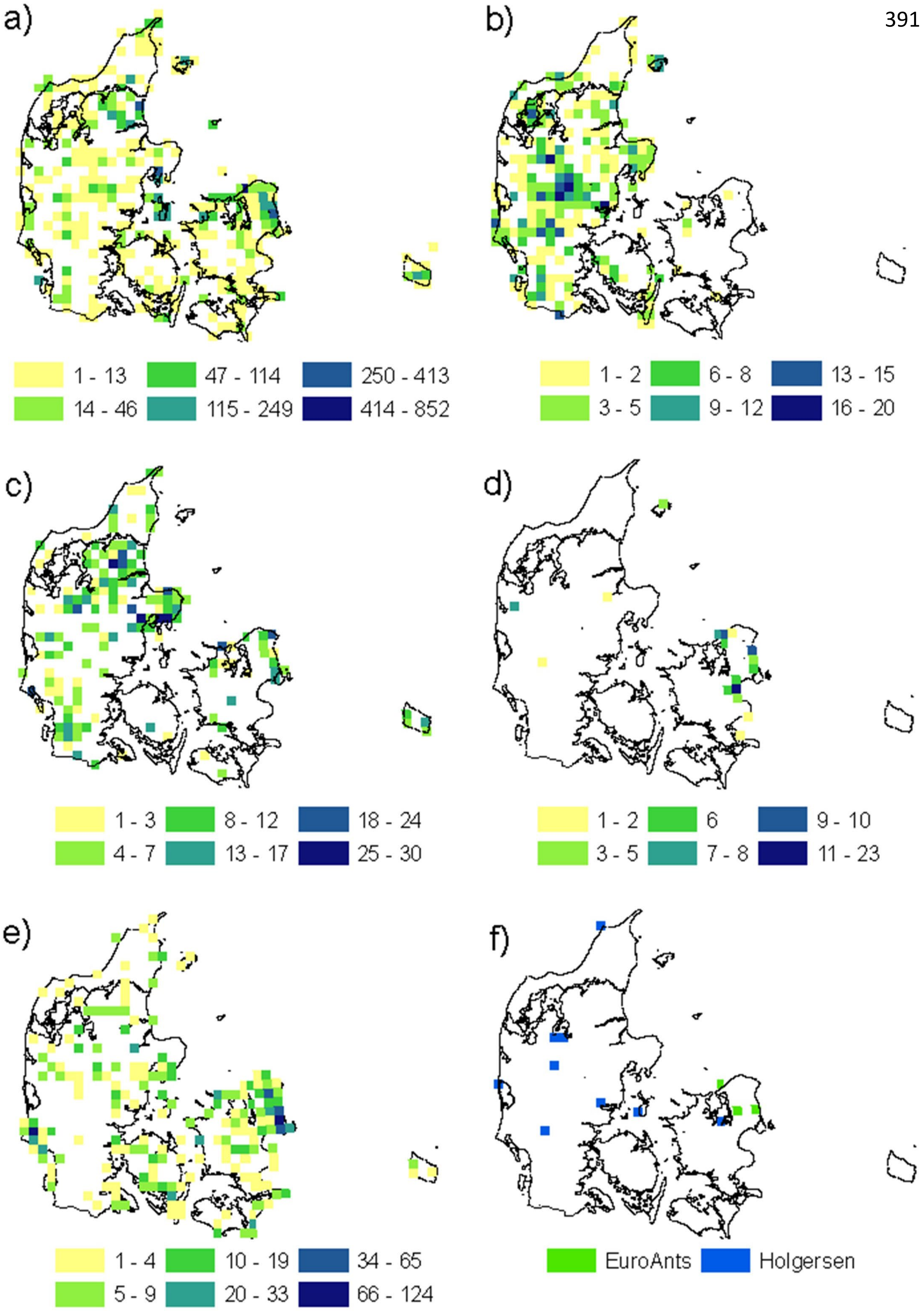


Figure S3: The proportion of visits that consist of a detection of a single species, two species, three species, or more than three species for the seven individual data sets grouped by datatype. A visit is a unique combination of site, here a 10x10 km grid cell, and a date, here between 1900 and 2019. Data sets from the Natural History Museum of Aarhus, the Natural History Museum of Denmark, Christian Skøtt, Holger Holgersen, Sämi Schär and the Ant Hunt all had a median list length of 1 (mean = 1.49, 1.53, 1.06, 1.64, 1.54 and 1.33, respectively). The EuroAnts course had a median list length of 8 (mean = 9.09).

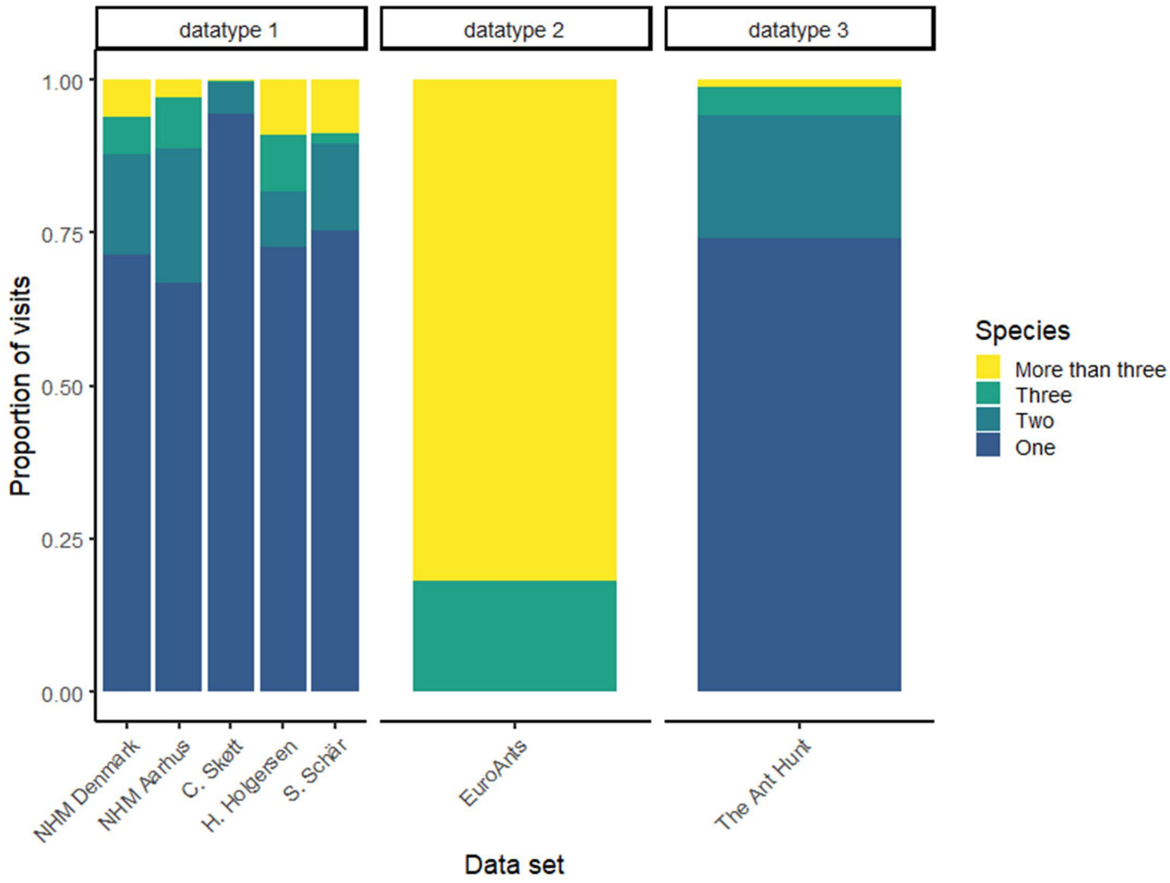
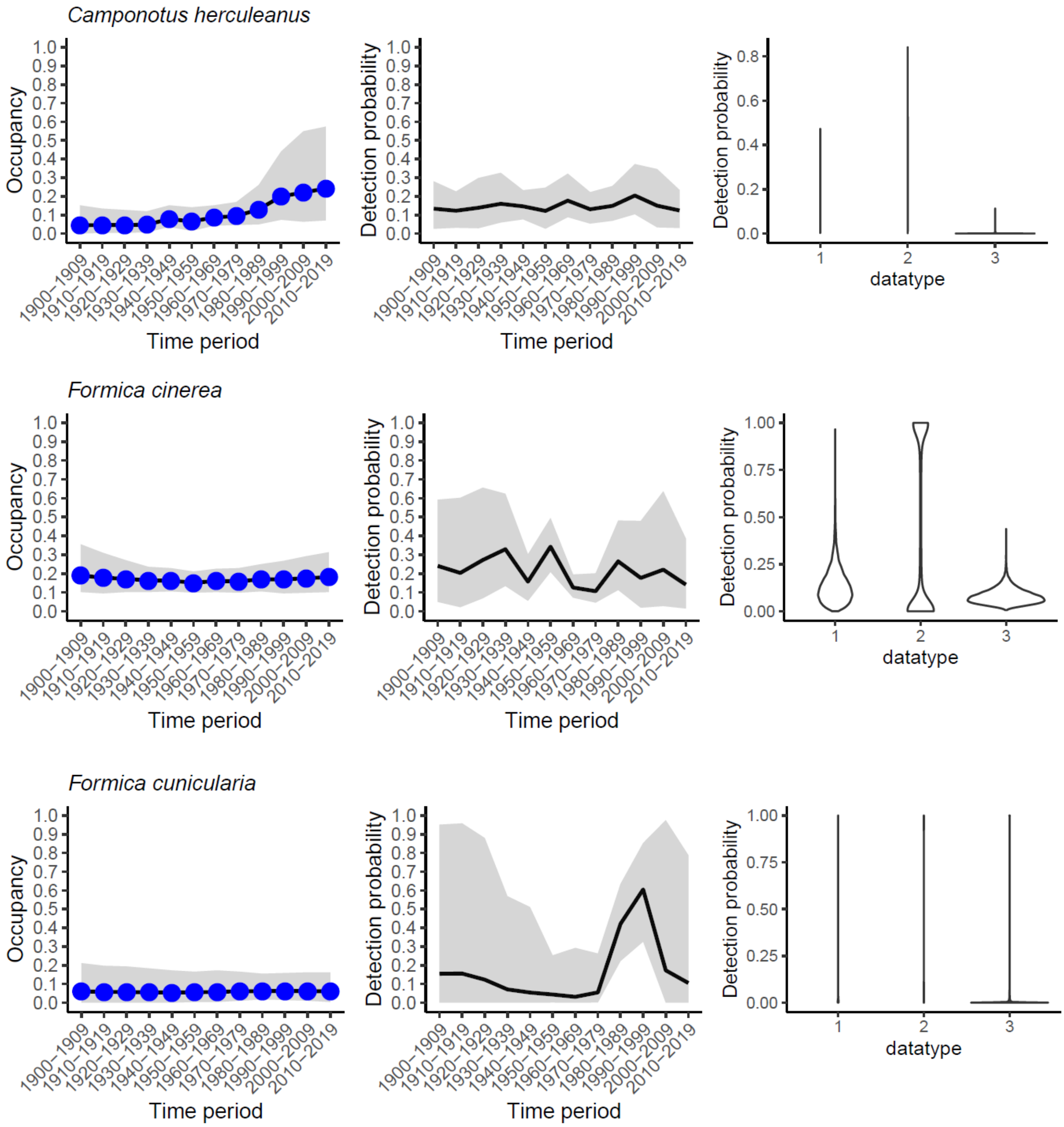
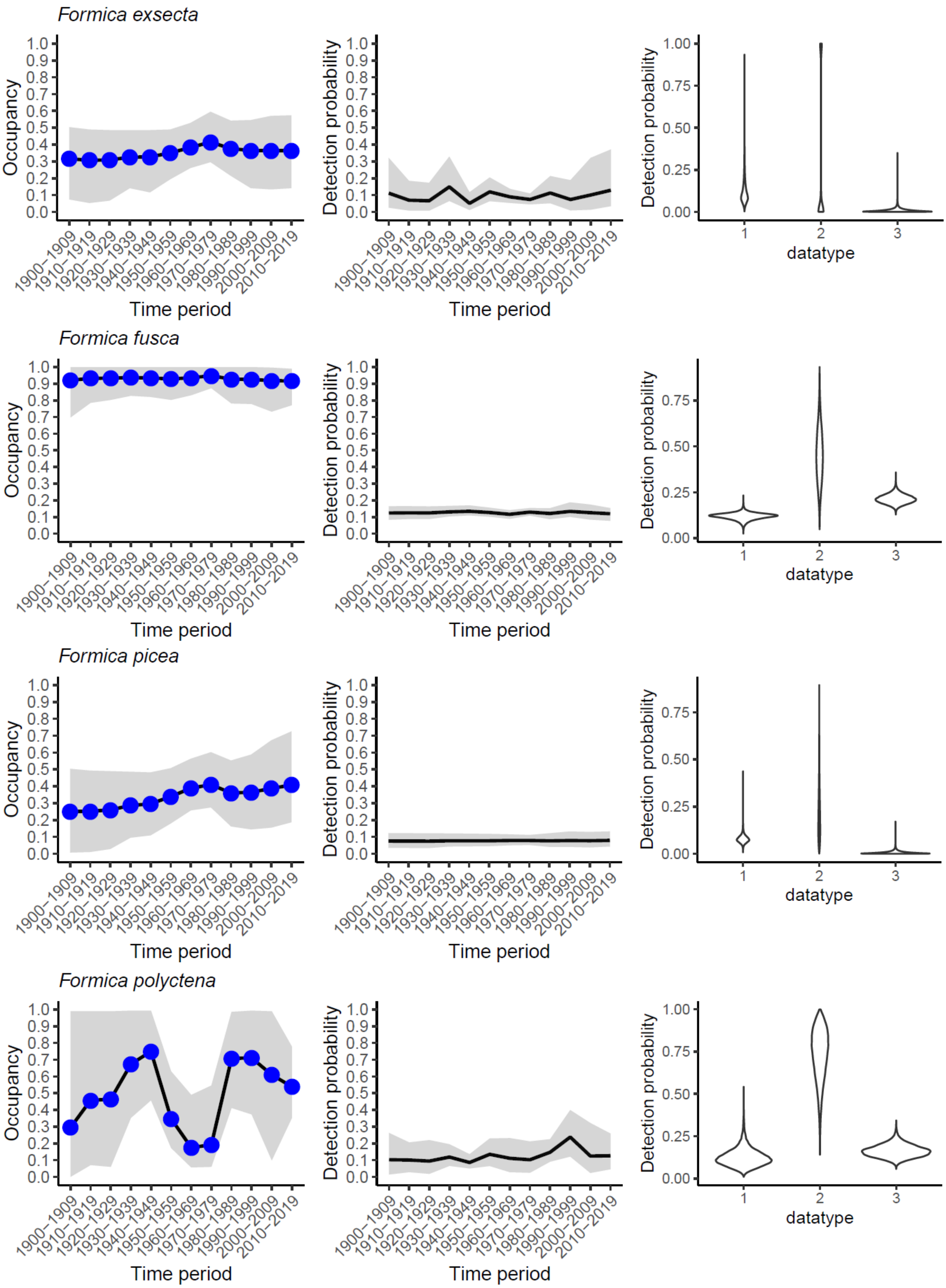
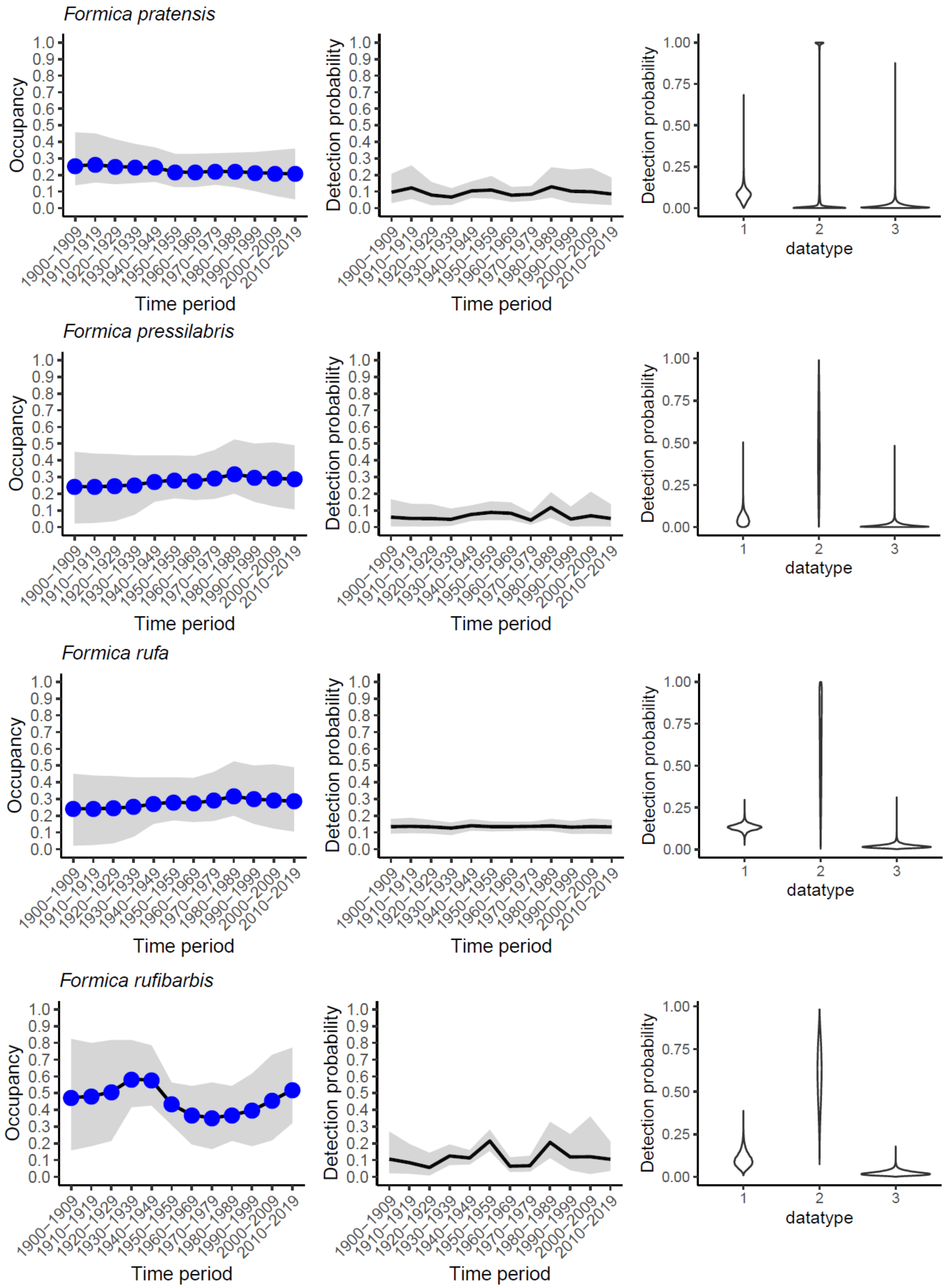


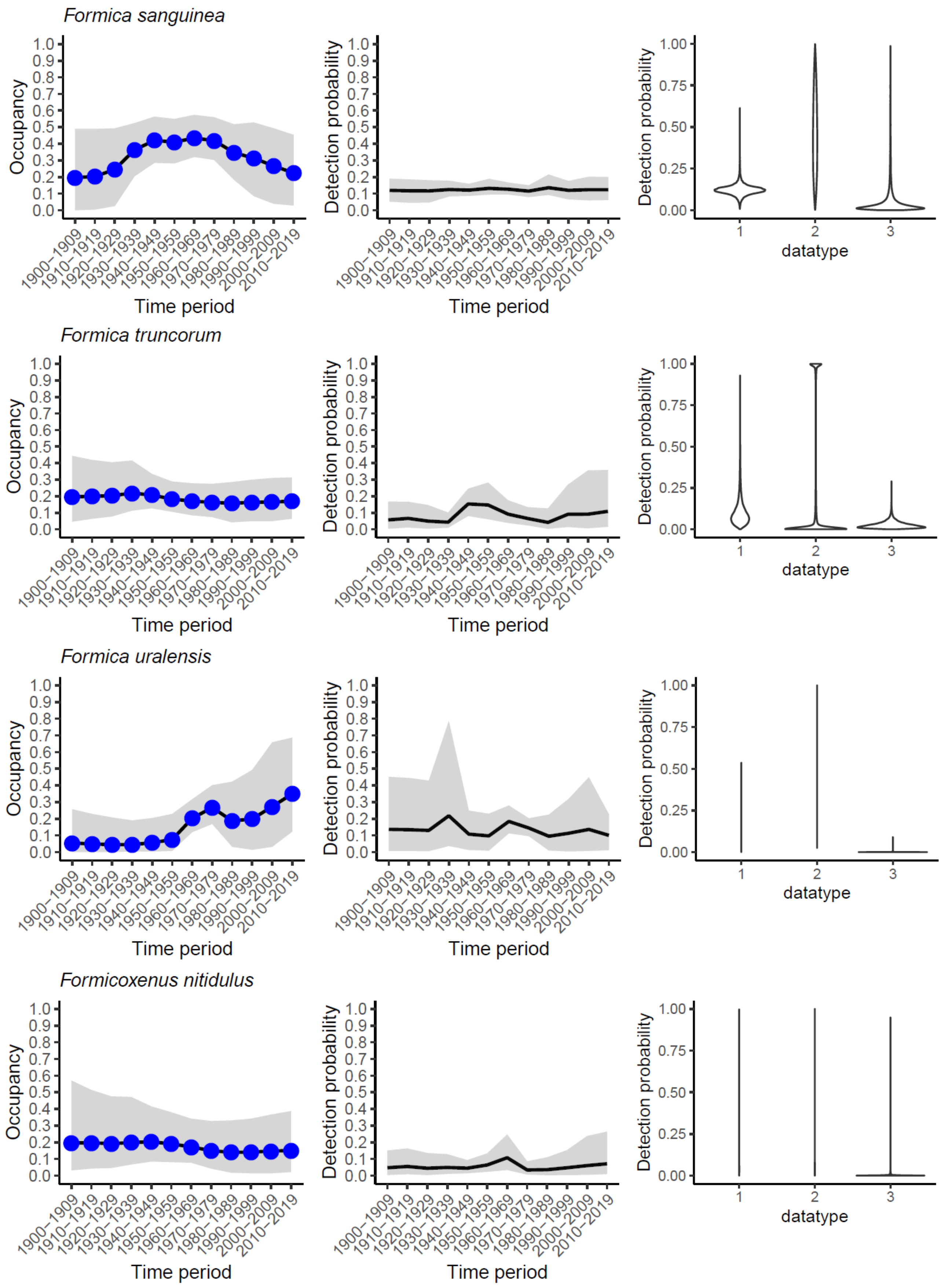
Figure S4: Decadal occupancy and detection probability for 29 ant species in Denmark from 1900-2019. The first column shows estimated occupancy for each decade. Blue dots indicate that models have converged (Rhat < 1.1). Solid lines represent the average values and the shaded area is the associated 95 % credible interval. The second column shows detection probability generated by the plot_DetectionOverTime function in the package Sparta for ListLength category 1 (The Natural History Museum of Denmark, the Natural History Museum of Aarhus, Holger Holgersen, Sämi Schär and Christian Skøtt), defined by the at parameter. Solid lines represent the average values and the shaded area is the associated 95 % credible interval. The third column shows detection probability for the last decade (2010-2019) for each of the three datatypes (1 =the Natural History Museum of Denmark, the Natural History Museum of Aarhus, Holger Holgersen, Sämi Schär, Christian Skøtt. 2 = the EuroAnts course and 3 = the Ant Hunt citizen science project). The difference between categories 2 and 3 are defined by parameters $ß_1$ and $ß_2$.

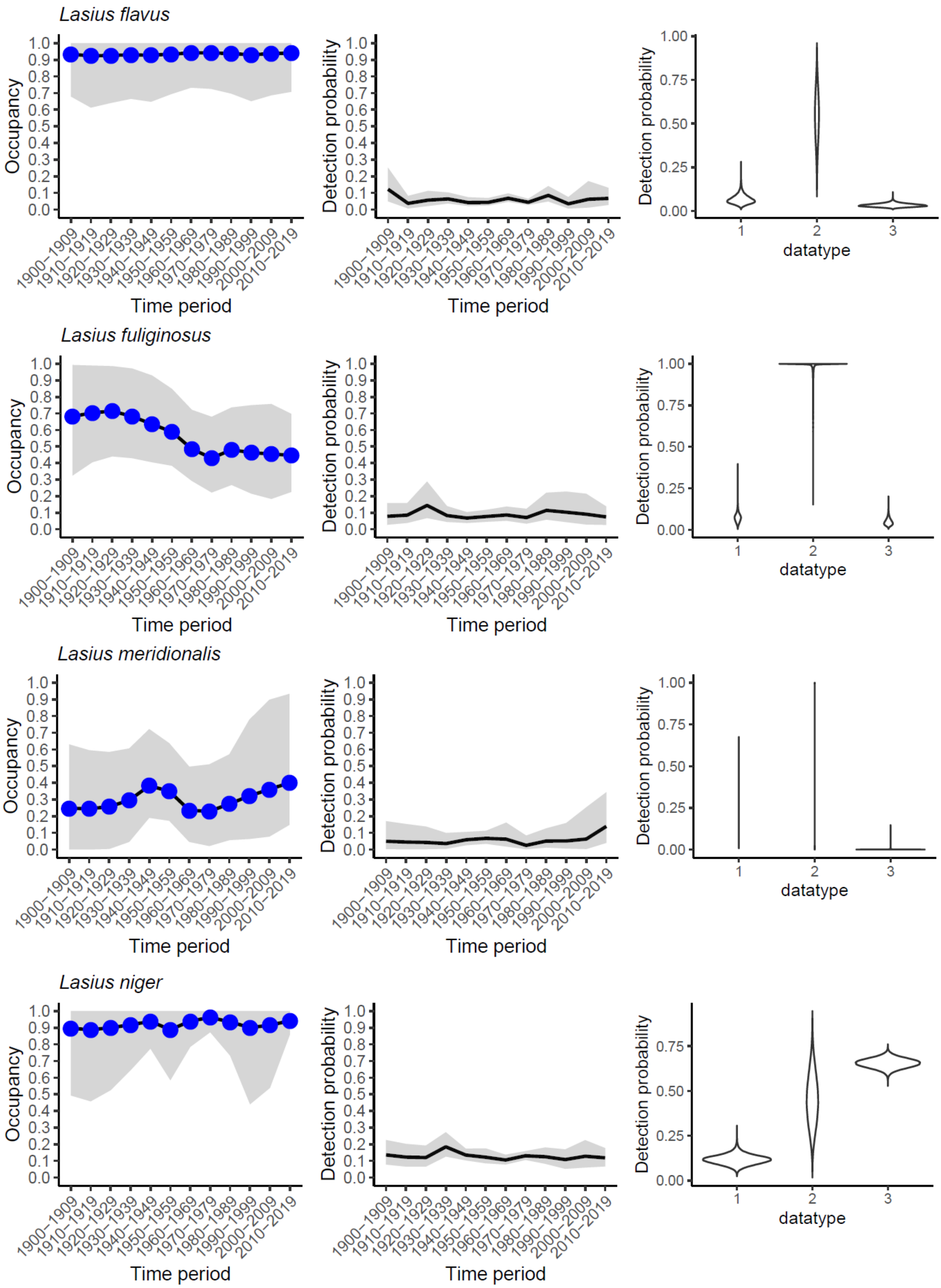


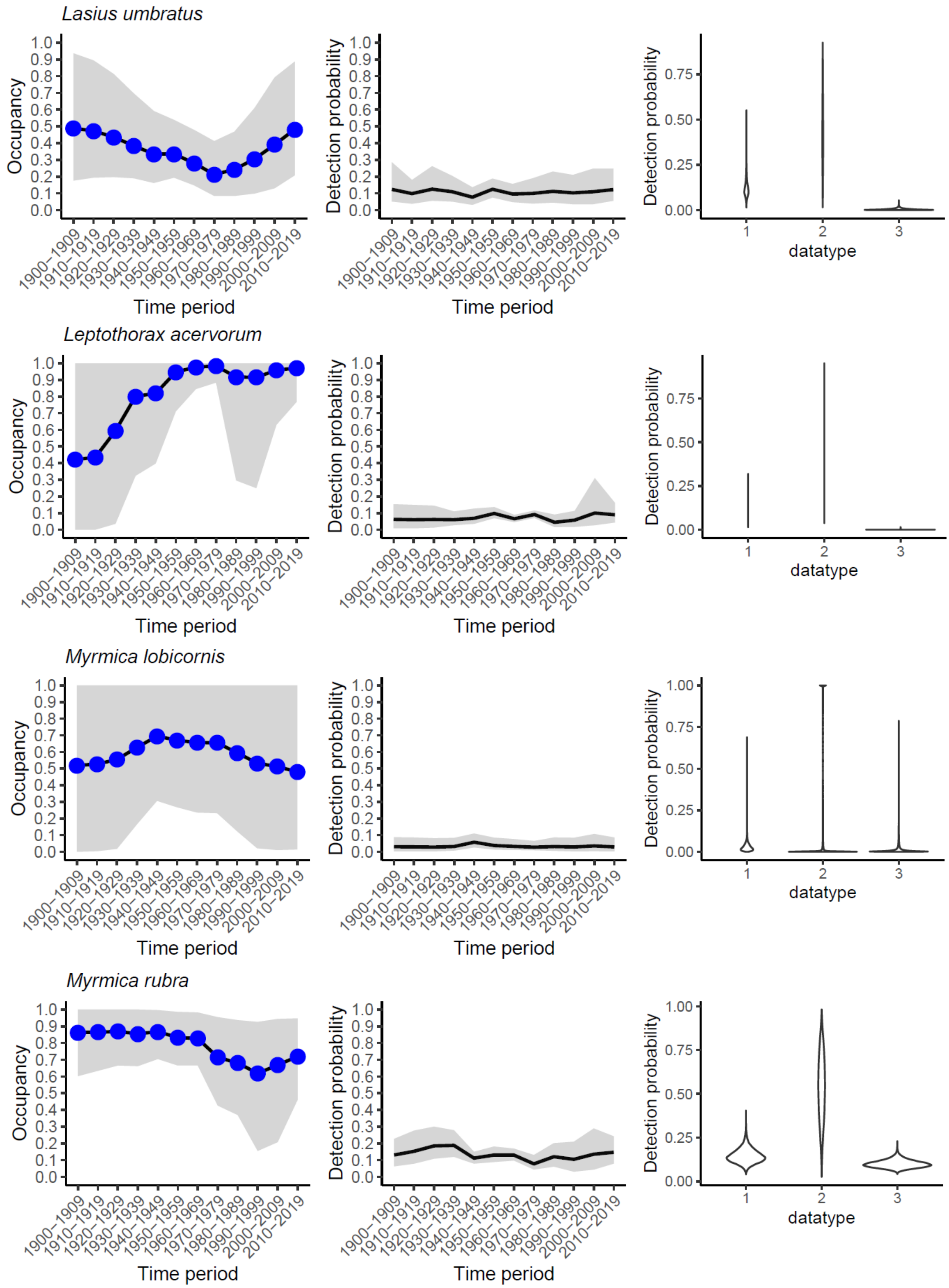


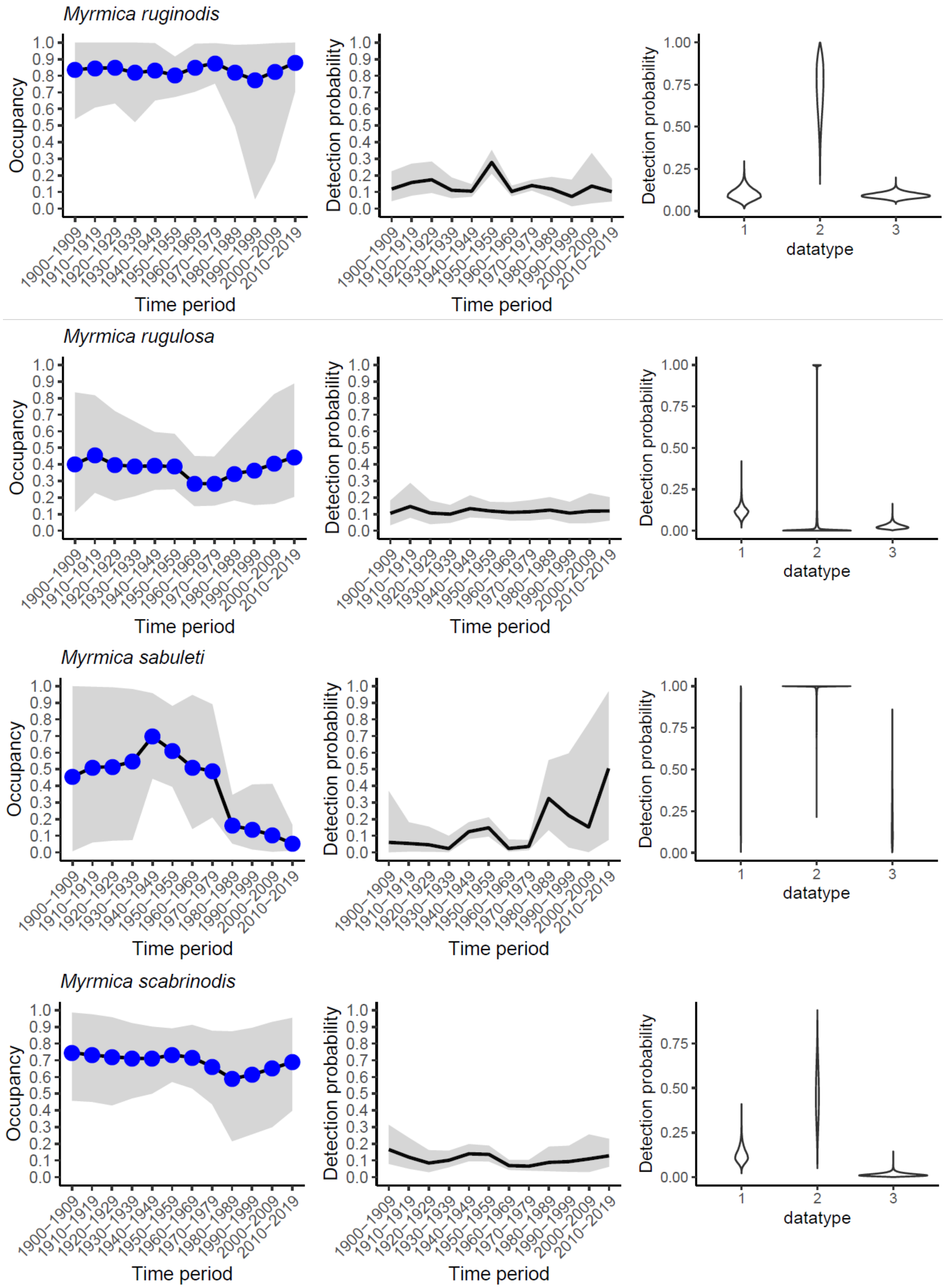
Formica exsecta
Occupancy
Detection probability
Time period
datatype
Formica fusca
Formica picea
Formica polyctena
1900–1909
1910–1919
1920–1929
1930–1939
1940–1949
1950–1959
1960–1969
1970–1979
1980–1989
1990–1999
2000–2009
2010–2019

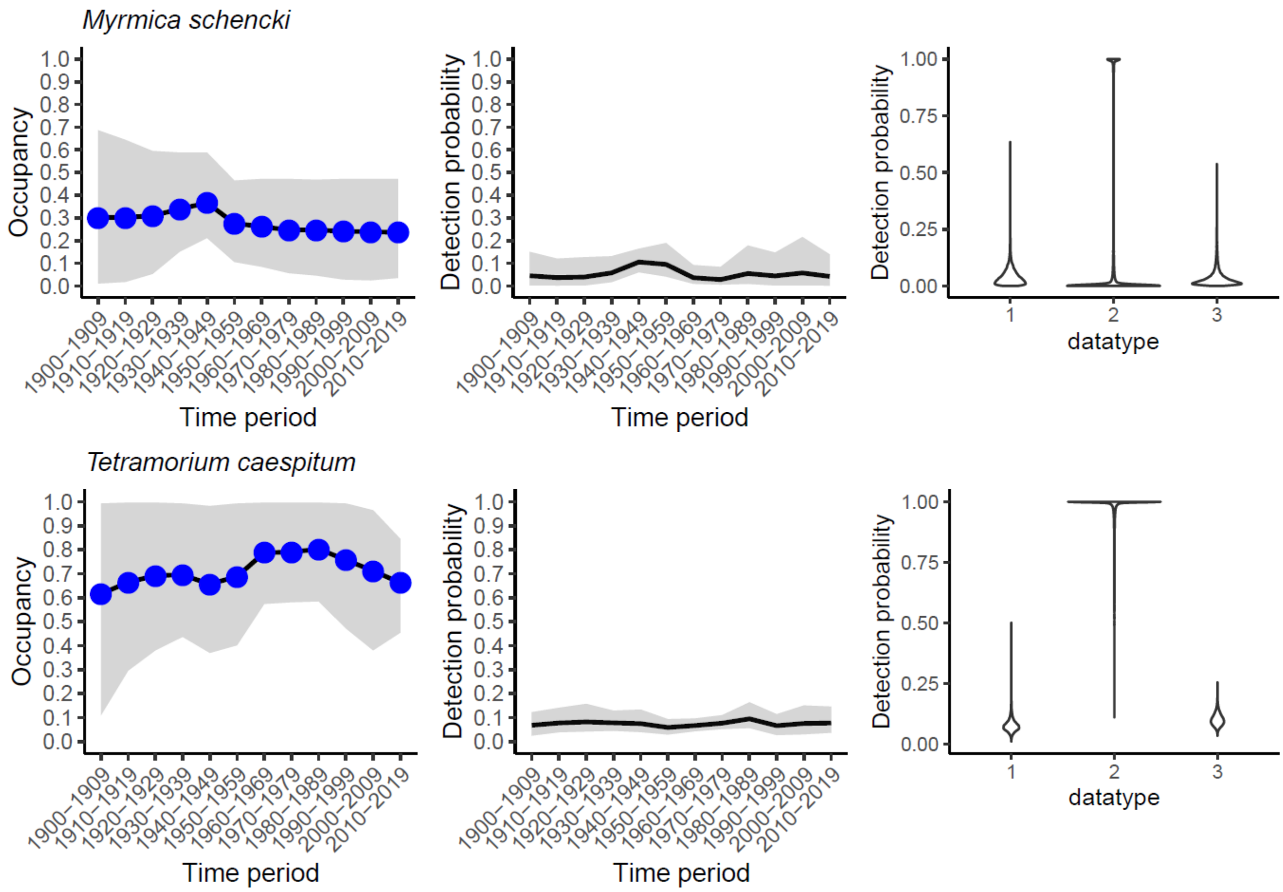

Formica pratensis
Formica pressilabris
Formica rufa
Formica rufibarbis
Occupancy
Detection probability
Time period
datatype
1900–1909
1910–1919
1920–1929
1930–1939
1940–1949
1950–1959
1960–1969
1970–1979
1980–1989
1990–1999
2000–2009
2010–2019


Formica sanguinea
Formica truncorum
Formica uralensis
Formicoxenus nitidulus
Occupancy
Detection probability
Time period
datatype
1900–1909
1910–1919
1920–1929
1930–1939
1940–1949
1950–1959
1960–1969
1970–1979
1980–1989
1990–1999
2000–2009
2010–2019
1
2
3
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
0.00
0.25
0.50
0.75
1.00


Lasius flavus
Occupancy
Time period
Detection probability
Time period
Detection probability
datatype
Lasius fuliginosus
Occupancy
Time period
Detection probability
Time period
Detection probability
datatype
Lasius meridionalis
Occupancy
Time period
Detection probability
Time period
Detection probability
datatype
Lasius niger
Occupancy
Time period
Detection probability
Time period
Detection probability
datatype


Lasius umbratus
Leptothorax acervorum
Myrmica lobicornis
Myrmica rubra
Occupancy
Detection probability
Time period
datatype
1900–1909
1910–1919
1920–1929
1930–1939
1940–1949
1950–1959
1960–1969
1970–1979
1980–1989
1990–1999
2000–2009
2010–2019


Myrmica ruginodis
Myrmica rugulosa
Myrmica sabuleti
Myrmica scabrinodis
Occupancy
Detection probability
Time period
datatype
1900–1909
1910–1919
1920–1929
1930–1939
1940–1949
1950–1959
1960–1969
1970–1979
1980–1989
1990–1999
2000–2009
2010–2019


Myrmica schencki
Occupancy
Time period
Detection probability
Time period
Detection probability
datatype
Tetramorium caespitum
Occupancy
Time period
Detection probability
Time period
Detection probability
datatype
1900–1909
1910–1919
1920–1929
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1940–1949
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1960–1969
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1980–1989
1990–1999
2000–2009
2010–2019

Table S5: Species suitability for modelling

Calculations of two metrics used to determine whether there is sufficient data to warrant occupancy modelling for each species in the two largest datasets individually and the combined dataset. The two metrics were the number of records of the focal species in the 10 % best recorded decades (90th percentile) and the proportion of total recording visits within the dataset that resulted in non-detections for the focal species, determined to be the best at describing suitability according to Pocock et al. 2019. Species were determined to be suitable for occupancy modelling if either 1) the proportion of visits with non-detection of the focal species was < 0.958 and the 90th percentile number of detections within a decade was ≥ 29 or 2) if the proportion of visits with non-detection of the focal species was ≥ 0.958 and the 90th percentile number of detections within a decade was ≥ 9.5.

	NHM Denmark			NHM Aarhus			all data sets combined		
Species	90% detections	prop. non-detection	suitable?	90% detections	prop. non-detection	suitable?	90% detections	prop. non-detection	suitable?
Camponotus herculeanus	6.4	0.976	no	1	0.991	no	8.3	0.984	no
Camponotus ligniperda	2	0.995	no			no	2.6	0.997	no
Formica cinerea	12.4	0.961	yes			no	17.2	0.974	yes
Formica clara			no			no	4	0.998	no
Formica cunicularia	8.6	0.984	no			no	8.6	0.992	no
Formica exsecta	11.2	0.969	yes	1	0.987	no	19.5	0.970	yes
Formica foreli			no			no	3	0.999	no
Formica forsslundi	1	0.998	no			no	1	0.999	no
Formica fusca	43	0.859	yes	13	0.847	no	77.3	0.856	yes
Formica gagatoides			no	1	0.991	no	1	0.999	no
Formica lugubris	1	0.999	no			no	1	0.999	no
Formica picea	7.4	0.979	no			no	20.9	0.972	yes
Formica polyctena	20.4	0.921	no			no	23.3	0.947	no
Formica pratensis	10.6	0.966	yes	1.9	0.987	no	13.2	0.975	yes
Formica pressilabris	11	0.969	yes	1	0.996	no	12	0.978	yes
Formica rufa	36.3	0.888	yes	21	0.790	no	63	0.892	yes
Formica rufibarbis	30.6	0.907	yes	1	0.991	no	28.9	0.944	no
Formica sanguinea	19.8	0.928	no	1	0.991	no	32.6	0.947	yes
Formica truncorum	12	0.973	yes	1	0.991	no	11.5	0.983	yes
Formica uralensis	10.8	0.980	no	1	0.996	no	18.6	0.982	yes
Formicoxenus nitidulus	6.6	0.985	no	1	0.996	no	6.8	0.991	no
Harpagoxenus sublaevis	3.9	0.995	no			no	5.9	0.996	no
Hypoponera punctatissima	3.8	0.992	no			no	5.5	0.994	no
Lasius alienus			no			no	2	0.999	no
Lasius brunneus	3.6	0.995	no	1	0.996	no	3.2	0.997	no

Lasius flavus	16	0.948	no	5.4	0.934	no	32.2	0.937	yes
Lasius fuliginosus	14.4	0.946	no	4	0.952	no	18	0.957	no
Lasius meridionalis	10.6	0.973	yes			no	10.2	0.984	yes
Lasius mixtus	2.5	0.992	no			no	2.5	0.995	no
Lasius niger	40	0.863	yes	11.5	0.856	no	81	0.798	yes
Lasius platythorax			no			no	42	0.984	yes
Lasius psammophilus			no			no	10	0.996	no
Lasius umbratus	10.6	0.957	no	3	0.948	no	13	0.968	yes
Leptothorax acervorum	21.2	0.937	no	2.6	0.978	no	40.8	0.932	yes
Leptothorax muscorum	1	0.999	no			no	2	0.999	no
Myrmecina graminicola			no	1	0.996	no	1	1.000	no
Myrmica lobicornis	13	0.973	no			no	12.6	0.981	yes
Myrmica rubra	30.7	0.892	yes	15.5	0.795	no	42.8	0.896	yes
Myrmica ruginodis	27.2	0.908	no	38.8	0.594	yes	76.4	0.877	yes
Myrmica rugulosa	16.6	0.953	no	4.6	0.930	no	18.1	0.962	yes
Myrmica sabuleti	33.9	0.932	yes	1	0.996	no	33.3	0.957	yes
Myrmica scabrinodis	33.2	0.920	yes	5.5	0.891	no	37	0.930	yes
Myrmica schencki	15	0.971	yes	1	0.996	no	14.4	0.982	yes
Myrmica specioides	1	0.998	no			no	1	0.999	no
Myrmica sulcinodis	3.2	0.993	no	1	0.996	no	8	0.993	no
Stenamma debile or *S. westwoodii*			no	1	0.996	no	1	1.000	no
Temnothorax interruptus	2.6	0.996	no			no	2.6	0.998	no
Temnothorax nylanderi	1	0.999	no			no	1	0.999	no
Temnothorax parvulus			no			no	1	1.000	no
Temnothorax tuberum	1.8	0.997	no			no	1.8	0.998	no
Tetramorium atratulum	1	0.999	no			no	1	1.000	no
Tetramorium caespitum	14	0.943	no	3.6	0.969	no	30	0.940	yes
Suitable species			14			1			24

Table S6: Overview of all analysed species, including number of iterations needed to reach convergence, Rhat values, Precision, mean occupancy in each time period, directional occupancy change, 95 % equal-tailed credible intervals and confidence of change. Confidence above 80 %, indicating occupancy change, has been highlighted in bold.

										Mean occupancy											
Species	**Iterations**	**$Rhat_{mean}$**	**$Rhat_{min}$**	**$Rhat_{max}$**	**Precision**	**Time Period**	**Change**	**95% ETI**	**Confidence**	**1900-1909**	**1910-1919**	**1920-1929**	**1930-1939**	**1940-1949**	**1950-1959**	**1960-1969**	**1970-1979**	**1980-1989**	**1990-1999**	**2000-2009**	**2010-2019**
Stable species																					
F. cinerea	50000	1.016	1.003	1.029	0.034	1900-1909 to 1950-1959	-0.04	-0.22, 0.04	73	0.190	0.178	0.172	0.164	0.162	0.151						
						1950-1959 to 2010-2019	0.03	-0.05, 0.18	68							0.160	0.160	0.169	0.169	0.175	0.181
F. cunicularia	50000	1.066	1.038	1.100	0.009	1900-1909 to 1940-1949	-0.006	-0.08, 0.03	45	0.060	0.058	0.057	0.055	0.054							
						1940-1949 to 1990-1999	0.008	-0.05, 0.08	59						0.055	0.058	0.061	0.062	0.063		
						1990-1999 to 2010-2019	-0.002	-0.06, 0.05	48											0.062	0.061
F. exsecta	200000	1.015	1.008	1.020	0.026	1900-1909 to 1910-1919	-0.009	-0.15, 0.09	51	0.316	0.307										
						1910-1919 to 1970-1979	0.11	-0.04, 0.47	77			0.309	0.325	0.327	0.350	0.383	0.414				
						1970-1979 to 1990-1999	-0.05	-0.36, 0.07	65									0.377	0.364		
						1990-1999 to 2000-2009	0.0004	-0.13, 0.14	47											0.365	
						2000-2009 to 2010-2019	-0.0009	-0.14, 0.14	47												0.364
F. fusca	100000	1.006	1.002	1.010	8.634	1900-1909 to 1930-1939	0.02	-0.07, 0.22	49	0.921	0.932	0.934	0.937								
						1930-1939 to 1950-1959	-0.008	-0.12, 0.07	51					0.934	0.929						
						1950-1959 to 1970-1979	0.02	-0.04, 0.15	62							0.936	0.948				
						1970-1979 to 2010-2019	-0.03	-0.20, 0.05	66									0.927	0.926	0.918	0.917
F. pratensis	100000	1.020	1.007	1.032	0.009	1900-1909 to 1910-1919	0.005	-0.08, 0.11	52	0.256	0.261										
						1910-1919 to 1960-1969	-0.04	-0.25, 0.04	73			0.251	0.247	0.244	0.218	0.215					
						1960-1969 to 1970-1979	0.007	-0.04, 0.08	54								0.222				
F. pressilabris	50000	1.013	1.001	1.035	0.013	1900-1909 to 1910-1919	-0.001	-0.09, 0.08	46	0.243	0.242										
						1910-1919 to 1950-1959	0.04	-0.10, 0.27	63			0.245	0.252	0.270	0.281						
						1950-1959 to 1960-1969	-0.005	-0.12, 0.08	50							0.276					
						1960-1969 to 1980-1989	0.04	-0.05, 0.26	69								0.291	0.317			
						1980-1989 to 2010-2019	-0.03	-0.28, 0.11	59										0.298	0.293	0.286
F. truncorum	50000	1.008	1.001	1.017	0.039	1900-1909 to 1930-1939	0.02	-0.14, 0.23	61	0.197	0.199	0.203	0.219						0.162	0.165	0.169
						1930-1939 to 1980-1989	-0.06	-0.29, 0.05	77					0.207	0.182	0.170	0.162	0.158			
						1980-1989 to 2010-2019	0.01	-0.09, 0.16	53										0.162	0.165	0.169
F. nitidulus	50000	1.009	1.002	1.015	0.139	1900-1909 to 1910-1919	0.001	-0.15, 0.13	51	0.196	0.197										
						1910-1919 to 1920-1929	-0.005	-0.16, 0.11	49			0.192									
						1920-1929 to 1940-1949	0.011	-0.18, 0.19	57				0.199	0.202							
						1940-1949 to 1980-1989	-0.063	-0.31, 0.07	75						0.191	0.172	0.150	0.139			
						1980-1989 to 2010-2019	0.012	-0.11, 0.18	52										0.141	0.147	0.151

Species	Iterations	$Rhat_{mean}$	$Rhat_{min}$	$Rhat_{max}$	Precision	Time Period	Change	95% ETI	Confidence	Mean occupancy											
										1900-1909	1910-1919	1920-1929	1930-1939	1940-1949	1950-1959	1960-1969	1970-1979	1980-1989	1990-1999	2000-2009	2010-2019
						1930-1939 to 1940-1949	-0.002	-0.10, 0.07	26					0.927							
						1940-1949 to 1970-1979	0.01	-0.05, 0.22	32						0.934	0.942	0.942				
						1970-1979 to 1990-1999	-0.01	-0.14, 0.06	28									0.937	0.931		
						1990-1999 to 2010-2019	0.01	-0.06, 0.13	28											0.937	0.941
L. meridionalis	600000	1.023	1.004	1.047	24.455	1900-1909 to 1910-1919	-0.003	-0.21, 0.16	45	0.248	0.244										
						1910-1919 to 1940-1949	0.14	-0.14, 0.63	72			0.257	0.295	0.382							
						1940-1949 to 1970-1979	-0.15	-0.61, 0.06	78						0.350	0.235	0.229				
						1970-1979 to 2010-2019	0.17	-0.08, 0.83	75									0.273	0.321	0.361	0.400
L. niger	400000	1.006	1.003	1.011	519.021	1900-1909 to 1910-1919	-0.009	-0.26, 0.19	43	0.897	0.888										
						1910-1919 to 1940-1949	0.05	-0.10, 0.44	51			0.900	0.918	0.938							
						1940-1949 to 1950-1959	-0.05	-0.35, 0.06	59						0.889						
						1950-1959 to 1970-1979	0.07	-0.03, 0.39	68							0.939	0.962				
						1970-1979 to 1990-1999	-0.06	-0.54, 0.05	62									0.935	0.901		
L. acervorum	100000	1.030	1.004	1.087	11.325	1900-1909 to 1970-1979	0.56	0.00, 1.00	72	0.421	0.435	0.594	0.801	0.819	0.947	0.977	0.983				
						1970-1979 to 1990-1999	-0.07	-0.72, 0.04	33									0.918	0.915		
						1990-1999 to 2010-2019	0.06	-0.10, 0.69	31											0.958	0.971
M. lobicornis	200000	1.046	1.024	1.053	997.235	1900-1909 to 1940-1949	0.18	-0.20, 0.91	64	0.519	0.527	0.555	0.627	0.695							
						1940-1949 to 2010-2019	-0.21	-0.93, 0.24	70						0.670	0.656	0.655	0.595	0.533	0.512	0.481
M. scabrinodis	50000	1.008	1.002	1.020	1.781	1900-1909 to 1940-1949	-0.04	-0.34, 0.23	60	0.746	0.731	0.721	0.712	0.710							
						1940-1949 to 1950-1959	0.02	-0.13, 0.24	56						0.732						
						1950-1959 to 1980-1989	-0.14	-0.56, 0.11	79							0.717	0.661	0.589			
						1980-1989 to 2010-2019	0.01	-0.14, 0.57	71										0.614	0.651	0.689

Figure S7: a) Effect of the number of detections in a decade for each individual species on uncertainty in occupancy, measured as the width of the 68% credible interval (1 standard deviation either side of the mean). b) Effect of occupancy estimate on uncertainty. The model performs with highest uncertainty at medium commonness. c) Effect of the modelled decade on uncertainty. Uncertainty is lowest for the last decades and the middle of the 20th century (but the effect is weak).