

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B

BIOLOGICAL SCIENCES

Brood parasitism in eusocial insects (Hymenoptera): role of host geographic range size and phylogeny

Journal:	<i>Philosophical Transactions B</i>
Manuscript ID	RSTB-2018-0203.R2
Article Type:	Research
Date Submitted by the Author:	n/a
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Issue Code (this should have already been entered but please contact the Editorial Office if it is not present):	BROOD
Subject:	Ecology < BIOLOGY, Evolution < BIOLOGY
Keywords:	Hymenoptera, social parasite, phylogeny, geographical range size, host parasite interactions, conservation biology

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3 **Brood parasitism in eusocial insects (Hymenoptera): role of host geographic range size**
4 **and phylogeny**
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24 7771
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27 **Keywords:** Hymenoptera, social parasite, geographic range size, phylogeny, host–parasite
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Summary

Interspecific brood parasitism is common in many animal systems. Brood parasites enter the nests of other species and divert host resources for producing their own offspring, which can lead to strong antagonistic parasite–host coevolution. Here, we look at commonalities among social insect species that are victims of brood parasites, and use phylogenetic data and information on geographic range size to predict which species are most likely to fall victims to brood parasites in the future. In our analyses, we focus on three eusocial hymenopteran groups and their brood parasites: (i) bumblebees, (ii) *Myrmica* ants, and (iii) vespine and polistine wasps. In these groups some, but not all, species are parasitized by obligate workerless inquilines that only produce reproductive-caste descendants. We find phylogenetic signals for geographic range size and the presence of parasites in bumblebees, but not in ants and wasps. Phylogenetic logistic regressions indicate that the probability of being attacked by one or more brood parasite species increases with the size of the geographic range in bumblebees, but the effect is statistically only marginally significant in ants. However, non-phylogenetic logistic regressions suggest that bumblebee species with the largest geographic range sizes may have a lower likelihood of harboring social parasites than do hosts with medium-sized ranges. Our results provide new insights into the ecology and evolution of host–social parasite systems, and indicate that host phylogeny and geographic range size can be used to predict threats posed by social parasites, as well to design efficient conservation measures for both hosts and their parasites.

1. Introduction

Due to anthropogenically induced environmental changes, such as global warming, habitat destruction and pesticide use, species are increasingly becoming threatened [1-5]. This creates a need for intensified conservation efforts, but to effectively protect species, we need to know their habitat requirements and ecological features [1,2,6]. Protecting existing habitats is a logical first step, but because species may be able to shift their habitat requirements and therefore improve their chance of survival, alternative and perhaps less preferred habitats should also be protected [7]. However, identifying potential alternative habitats may be very difficult, calling for a viable method for assessing the usefulness of both existing and potential resources and habitats.

In the case of parasitic species, different host species constitute alternative habitats. Depending on the parasite species, the number of habitats (i.e. host species) varies from one (specialist) to many (generalist). When host numbers decline, e.g. due to environmental deterioration, a parasite species may start using one or more additional hosts (host-range expansion), evolve a preference for a completely different host (host switch) (Fig. 1)[8] or it may disappear altogether. However, the causes and consequences of host switches and host-range expansions have received very little attention [9], and it is currently unknown whether certain traits of host species could increase the likelihood of host switching or host-range expansions. To this end, we decided here to examine whether host switching and the presence of a parasite species could be predicted based on the combination of host phylogeny and geographic range size (hereafter GRS)[9].

According to the resource distribution hypothesis [10,11], widespread species are able to support a higher parasite diversity than are species with more restricted geographic ranges. Large GRS and large population size of host species have often been shown to correlate with high parasite prevalence and diversity [12-16], so that rare hosts tend to have fewer [8] or no [15] parasite species. However, it is poorly known how GRS and phylogenetic relationships among actual and potential host species affect the probability of host switching by parasites [9].

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3 There is a very tight coevolutionary relationship between hosts and their parasites, often
4 described as an arms race or the Red Queen hypothesis [6,17-20]: hosts try to evolve stronger
5 defensive capabilities, while parasites strive to increase their chances of successful infection
6 and reproductive success. Host–parasite arms races function as accelerants for trait evolution
7 [21-23], genetic divergence [21,24] and may eventually lead to speciation, especially if the
8 number of parasite species per host species is high [24]. Alternatively, a parasite species may
9 simply switch to a new host species. The likelihood of a successful shift is influenced by two
10 components: First, a shift is more probable if the new host species is closely related to the
11 current host(s) [9,20,25], as close relatives tend to share ecological traits and probably have
12 similar chemical signatures [19,26,27] (Fig. 1). Second, a large GRS and population size of
13 the new host increases the probability of long-term survival of the parasite [9] (Fig. 1).

22
23 To investigate the likelihood of parasitism and the probability of host switching in relation to
24 the GRS of host and non-host species, we selected three hymenopteran eusocial groups with
25 species harboring obligate interspecific workerless social parasites (‘inquilines’): bumblebees
26 (*Apidae: Bombus*), *Myrmica* ants (*Formicidae*) and wasps (*Vespidae: Vespinae* and
27 *Polistinae*). In these focal groups, the parasite species commandeer the nests of their hosts
28 and usurp their resources for reproduction of only sexual offspring, rendering the parasite
29 species completely dependent on provisioning by their hosts. Due to the tight relationship
30 between the inquilines and their hosts, it has been suggested that parasites would tend to be
31 close relatives of their host species. However, recent phylogenetic analyses have shown that
32 this hypothesis, generalized as Emery’s Rule [28,29], does not hold in a wider perspective. In
33 ants, inquilinism has evolved several times, which has resulted in a wide range of
34 phylogenetic relationships between parasites and their hosts as well as between different
35 parasite species [30,31]. In bumblebees, inquilinism is restricted to the subgenus *Psithyrus*,
36 making them all close relatives of each other [32]. Inquiline wasps likewise appear not to be
37 the closest relatives of their hosts, although they are from the same clade as their host species
38 [29].

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51 By re-analyzing previous studies on hosts and social parasites in bumblebees, *Myrmica* ants,
52 and vespine and polistine wasps, we created a large data set to answer the following
53 questions: i) does host GRS influence the presence and diversity of brood parasites, ii) do
54 obligate social parasite species have a tendency to parasitize the same host species, iii) are
55 closely related host species more similar in their parasitism than are hosts drawn at random,
56 and iv) can these results be used to predict the future parasitism of social insect species?
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3 Based on our previous results [15], we expected that host species with larger GRS are more
4 often parasitized than are species with narrower ranges. We also expected a tendency for
5 closely related species to be similarly parasitized or unparasitized [17] because previous
6 studies [33] have suggested a phylogenetic signal in GRS.
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10 11 12 13 2. Methods 14 15 16 17

18 Host and parasite data 19 20 21

22 We compiled a dataset on host species and interspecific brood parasites in *Bombus*
23 bumblebees, *Myrmica* ants, and vespine and polistine wasps based on a broad survey of
24 relevant ecological and taxonomic literature. The focal host taxa and species were selected so
25 that information is available on parasitism by social brood parasites, phylogenetic
26 relationships (see below), and GRS of actual and potential hosts. Parasite species were
27 considered if they are strict workerless inquiline, meaning that facultative inquilines were
28 excluded. In all, our dataset includes information on parasitism in 230 bumblebee species
29 [32-34] of which 182 have phylogenetic data [35], 63 ant [31,36,37], and 37 wasp species
30 [29,38,39] (Supplement Tables 1–3).
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45 For bumblebees, we considered cuckoo bumblebee species (*Bombus* subgenus *Psithyrus* spp.)
46 that produce only sexual castes (queens and males), but not workers [32]. A total of 24
47 *Psithyrus* species have been found in the nests of 34 of the focal 230 bumblebee species.
48 However, because direct observations of breeding inquiline queens are not available for all
49 presumed hosts [32], we performed statistical analyses using also a dataset that considered as
50 hosts only those 25 bumblebee species for which nests with breeding *Psithyrus* queens had
51 been found [32].
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Geographic range sizes were obtained by counting the number of 611 000 km² squares that each species occupies, based on data from [34] for bumblebees and AntMaps [40,41] for ants.

We added *Bombus glacialis* to one of our datasets due to the fact that it occurs only on two arctic islands [32]. Reliable data on GRS were not available for the focal wasp species.

Phylogenetic trees

To control for the effect of relatedness among species, which can confound comparative analyses [42,43], we estimated phylogenetic signal in GRS and parasitism and performed phylogenetic logistic regression based on ultrametric phylogenetic trees of actual and potential hosts. A time-calibrated phylogeny for *Bombus* from [35] was pruned down in Mesquite v. 3.40 [44] to 182 species for which data on parasitism and GRS were available. For *Myrmica* ants, we estimated an ultrametric tree based on the 3886-bp sequence data matrix and tree topology of Jansen et al. 2010 [31], both of which are available in TreeBase (<http://purl.org/phylo/treebase/phylows/study/TB2:S10277>). The original topology was ultrametricized based on penalized likelihood with the chronos command (correlated rate model with $\lambda = 1$) in the ape v.4.0 [45] package in R v.3.3.2 [46]. The resultant tree was then used as a starting tree and topological constraint in an analysis in BEAST v.2.5.1 [47], in which branch lengths were estimated by implementing a GTR+I+G substitution model and assuming an uncorrelated lognormal molecular clock. The analysis was run for 10 million steps while sampling trees and parameters every 1000 steps. After confirming in Tracer v.1.7.1 [48] that the run had converged and that ESS values were > 200 , the final Maximum clade credibility tree with median node heights was calculated in TreeAnnotator (part of the BEAST package) based on the 9001 trees sampled after a 10% burnin. Outgroups and species

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3 with missing data were then pruned in Mesquite, leaving a tree with 63 terminals. For vespine
4 and polistine wasps, we supplemented the 6568-bp sequence matrix of Lopez-Osorio et al.
5 [29] with 658 bp of COI barcode data downloaded from GenBank for four species (*Vespula*
6 *rufa* KU496858, *Dolichovespula alpicola* KM566926, *D. norwegica* HM860327 and *Vespa*
7 *velutina* JQ780455). A maximum-likelihood phylogeny including the additional species was
8 then calculated using RAxML BlackBox [49] on the CIPRES server [50] based on a GTR+G
9 substitution model. The resulting topology was then ultrametricized and used as a constraint
10 when re-estimating branch lengths in BEAST in the same way as described above for ants,
11 and, finally, parasite taxa were removed, leaving a tree with 37 actual and potential wasp host
12 species.
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Statistical analyses

33 Pagel's lambda (λ) [28,51] was used to measure phylogenetic signal in geographic range size
34 and in the number of social brood parasites per host species. A λ of 0 indicates that trait
35 values vary randomly across a phylogeny (i.e., absence of phylogenetic signal), while a value
36 of 1 indicates Brownian-motion evolution (i.e., the presence of phylogenetic signal) [51]. To
37 measure phylogenetic conservatism in the binary variable of whether a species is parasitized
38 or not, we used the D-statistic [52]. In this case, a D close to 0 indicates a phylogenetically
39 clustered pattern expected under a Brownian threshold model, while a value of 1 indicates a
40 phylogenetically random pattern [52]. These two metrics of phylogenetic signal perform well
41 in statistical tests for evolutionary trait conservatism [53]. We estimated index values and
42 tested for deviations from 0 and 1 in R, using the phytools package [54] for Pagel's λ and the
43 caper package [55] for the D-statistic.
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3 For bumblebee and ant species that were included in the phylogenetic trees, we used
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5 phylogenetic logistic regression models to assess whether species-specific GRS influences
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7 the presence of social brood parasites. Presence or absence of parasites was explained using
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9 GRS and GRS squared (GRS^2) using the `pgls` function of the `phylolm` v.2.6 package [56] in
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11 R.
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16 Analogous non-phylogenetic logistic regression analyses (for all bumblebee and ant species
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18 with data on parasitism and GRS) were performed using IBM SPSS for Windows v. 20.0. For
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20 the larger bumblebee dataset, we also investigated whether the GRS of a species can be used
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22 to estimate whether it is likely to be infected by brood parasites in the future, using the
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24 parasitism probabilities of different bumblebee species predicted by the non-phylogenetic
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26 logistic regression. We matched current host species with their closest unparasitized relatives
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28 (Supplementary Table 4), and then then compared GRS and estimated probability of
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30 parasitism across the two groups using paired-samples t-tests.
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3. Results

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36 Brood parasitism existed in all three hymenopteran groups to a varying degree. The number
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38 of cuckoo bumblebee species per bumblebee host varied from 0 to 4 (Fig. 2), with a mean of
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40 0.23 (SD = 0.62). The number of inquiline *Myrmica* ants per host species ranged from 0 to 3
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42 (Fig. 3), with an average of 0.24 (SD = 0.67). In the studied vespine and polistine wasps, each
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44 host species harbored a single parasite species, except for *Polistes dominula*, which is
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46 attacked by three inquiline species (Fig. 4.), the mean number of parasites per host species
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48 was 0.43 (SD = 0.64).
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54 In bumblebees, statistically significant phylogenetic signal was present for GRS and the
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56 presence of *Psithyrus* inquilines when considering all observations of parasitism, but not
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3 when considering only the smaller number of cases in which a breeding inquiline queen had
4 been observed; phylogeny had no effect on the number of parasite species (Table 1). In
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7 *Myrmica* ants, GRS varied randomly across the phylogeny, and phylogenetic signals for the
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10 existence of parasitism and the number of associated social parasite species were statistically
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12 only marginally significant. (Table 1). In the case of vespine and polistine wasps, both the
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14 existence of parasitism and the number of parasite species were random with respect to
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17 phylogeny (Table 1).
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20 According to our logistic and phylogenetic logistic regressions, the risk of being attacked by
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22 at least one social parasite species increases statistically significantly with GRS in both
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24 bumblebees and *Myrmica* ants, although the effect is statistically only marginally significant
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26 for ants when taking phylogeny into account (Table 2). However, the non-phylogenetic
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28 analyses based on all parasitized species as well as all species with direct observations of
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30 breeding inquiline queens suggest that bumblebee species with the largest GRS are less often
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32 parasitized than are species with a medium GRS (Fig. 5a; Table 2).
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Reflecting the results of the logistic regressions, average GRS of unparasitized bumblebee
species (10.8 grids, SD = 11.9, n = 196) was statistically significantly smaller than that of
parasitized species (30.9, SD = 15.8, n = 34; t-test with unequal variances, $t = -7.06$, $df =$
39.8, $P < 0.001$). Because the probability of social parasitism in bumblebee species was not
linear (Fig. 5a), we also compared the estimated probabilities of parasitism between
unparasitized and parasitized bumblebee species. This comparison revealed that the average
estimated probability of parasitism in unparasitized species (10.5 %, SD = 15.8 %, n = 196)
was smaller than in parasitized species (30.9 %, SD = 19.6, n = 34; t-test with unequal
variances, $t = -8.07$, $df = 41.8$, $P < 0.001$). Reanalyzing the data using only hosts for which

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3 nests with breeding *Psithyrus* queens had been found did not change these results (results not
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5 shown).
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8 In the case of *Myrmica* ants, the difference in average GRS of unparasitized (5.7 grids, SD =
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10 6.7, n = 54) and parasitized species (13.0, SD = 10.0, n = 9) was only marginally significant
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12 (t-test with unequal variances, $t = -2.11$, $df = 9.2$, $P = 0.064$).
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19 In 34 bumblebee species pairs consisting of closely related parasitized and unparasitized
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21 species (Supplementary Table 4), parasite-free species had on average a smaller GRS (17.4,
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23 SD = 15.2) than did their closest parasitized relative (30.9, SD = 15.8) (paired-samples t-test,
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25 $t = 4.21$, $df = 33$, $P < 0.001$; Fig. 6a). By contrast, in nine corresponding pairs of *Myrmica*
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27 ants, average GRS of non-parasitized species (13.0, SD = 10.0) did not differ statistically
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29 significantly from parasitized species (13.0, SD = 9.0) (paired-samples t-test, $t = 0.00$, $df = 8$,
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31 $P = 0.999$; Fig 6b).
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37 In pairwise analyses of the probability of parasitism estimated based on the non-phylogenetic
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39 logistic regression model, the estimated probability was on average lower in unparasitized
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41 (mean = 22.3 %, SD = 24.6 %, n = 34) than in parasitized (mean = 39.3 %, SD = 19.6 %) (n =
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43 34, paired-samples t-test, $t = 3.69$, $df = 33$, $P = 0.001$; Fig. 7.). Based on the pairwise plot,
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45 three of the studied parasitized bumblebee species (*B. argillaceus*, *B. bimaculatus* and *B.*
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47 *pascuorum*) have a low probability of parasitism (Fig. 7, sector A), while their currently non-
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49 parasitized relative has high probability of serving as a new potential hosts in the future (see
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51 also Supplementary Table 4). Two of the current host species (*B. lucorum* and *B. terrestris*)
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53 are not likely to lose their social parasites (Fig. 7 sector B). The situation is worst for cuckoo
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55 bumblebee species located in sector C of Figure 7: their host species have a high probability
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57 of losing their social brood parasites, but alternative host species are either not available or
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3 have a low estimated probability of parasitism (less than 50 % and in most of cases less than
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5 20 %; Fig. 7, sector C). A slightly better situation for cuckoo bumblebees is present within
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7 sector D of Fig. 7, as the current hosts are unlikely to lose their social brood parasite species.
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11 We found that 13 bumblebee species assumed to be unparasitized may in fact act as hosts for
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13 cuckoo bumblebees, as their model-based probability of parasitism is over 50% (Table 3).
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16 Three of these potential host species occur in the Holarctic region, seven in the Palearctic
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18 region and three in the Nearctic region. Furthermore, we found that 23 currently parasitized
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20 bumblebee species have a high probability of losing their social brood parasites in the future,
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22 as their estimated probability of parasitism is below 50% (Table 3). More than half (14) of
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24 these species occur in the Nearctic region, eight in the Palearctic region and only one in the
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26 Holarctic region (Table 3). The lowest estimated probability (7 %) of parasitism in an
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28 actually parasitized species was found for *B. affinis*, meaning that it may lose its inquiline *B.*
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30 *ashtoni*. Also, *B. appositus* is likely to lose its social brood parasites *B. insularis* and *B.*
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32 *flavidus* (Table 3).
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40 4. Discussion

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45 Our objective was to evaluate how host phylogeny and species-specific GRS influence the
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47 occurrence of brood parasitism in eusocial insects. We found five main results: First, the
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49 number of social brood parasite species varied widely among actual and potential hosts, so
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51 that most species are parasite-free, whereas others may be attacked by up to four different
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53 inquiline species. Second, geographic range size and the presence of one or more parasites
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55 were phylogenetically conserved in bumblebees, but phylogenetic signal was less clear or
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57 absent in *Myrmica* ants and vespine and polistine wasps. Third, phylogenetic logistic

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3 regressions showed that the probability of attack by one or more parasite species increased
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5 with GRS in bumblebees, but the effect was only marginally significant in ants; comparisons
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7 of range sizes across pairs of related parasitized and unparasitized species supported these
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9 conclusions. Fourth, non-phylogenetic logistic regressions suggested that parasitism increases
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11 with increasing range size in bumblebees and in *Myrmica* ants, but also that bumblebee
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13 species with the broadest distributions have a lower probability of being parasitized than
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15 species with a medium-sized range. Finally, we used our logistic regression model to estimate
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17 the likelihood parasitism or loss of parasites for specific bumblebee species. Our study
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19 provides new insights into brood parasitism of eusocial insects, how host GRS and phylogeny
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21 affect parasitism, how likely parasites are to switch among hosts, and how we can use this
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23 information for evaluating threats of host and parasite species in conservation biology.
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31 While most parasitized species are attacked by a single social parasite species, others harbor
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33 as many as four species. The most severely parasitized species are apparently very poor at
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35 defending against their parasites, either because their parasites are good at mimicking the
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37 chemical signatures of the host, or are otherwise able to evade the host's defences [19,26].
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39 Currently there is very little research on this topic, and it needs to be studied thoroughly in
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41 the future. In host species that are used by more than one brood parasite species, interspecific
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43 competition is likely to occur between the different parasite species. This will most likely
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45 reduce the reproductive success of all brood parasites and thereby lower their population
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47 sizes and the overall prevalence. In the long run, interspecific competition among parasites
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49 may even lead to extinction of weaker competitors, unless they are able to shift onto a new
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51 species. For the host species, multi-parasite attack is especially demanding because they need
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53 to defend themselves against two, three or even four parasite species. It seems unlikely that a
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55 host species could develop a defensive strategy that would be simultaneously effective
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3 against all parasite species. Therefore, it is likely that the main coevolutionary processes in
4 multispecies host–parasite systems involve interspecific competition between parasite species
5 rather than escalating defences and counter defences of hosts and parasites.
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12 The phylogenetic signal present in bumblebee parasitism and its tendency in *Myrmica* ants
13 suggest that brood parasite species have been able to among closely related hosts and non-
14 hosts. At least some social brood parasites, such as *Myrmica karavajevi*, are generalists
15 capable of using multiple host species. Such generalist parasite species may occasionally be
16 forced to shift from a previously exploited host to a new one. In our previous studies, we
17 have found phylogenetic signals in water mite and gregarine parasitism in damselfly and
18 dragonfly hosts [57]. This begs for further phylogenetic studies on other host–parasite
19 systems, in order to find possible general patterns. That vespine and polistine wasps did not
20 exhibit phylogenetic signal with regard to social brood parasitism suggests that their parasites
21 have not been restricted to shifting among closely related hosts in the past, at least not in the
22 extent that we expected. It is possible that wasp parasites are specialized to their host species,
23 to the extent that interspecific competition has not forced parasites to shift from host species
24 to another. Wasps are somewhat problematic for our study due to the lack of reliable
25 information on species-specific geographic ranges and due to the fact that some widely
26 distributed species, especially *Vespula germanica* and *V. vulgaris*, are invasive alien species
27 throughout most part of their range [58]. A larger dataset and more data on the distributions
28 of wasp species are required before we can rule out the possibility that the patterns we
29 observed in bumblebees and *Myrmica* ants do not occur in wasps.
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56 As expected, our different analyses consistently revealed that the GRS of bumblebee species
57 explains the occurrence of a brood parasite species reflecting this general pattern,
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3 unparasitized bumblebee species tended to have a smaller GRS than closely related
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5 parasitized species. Shifts onto new hosts that have a small GRS [15] may be rare because the
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7 chance of encounter may be low, but also because local abundance of species tends to drop
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9 with decreasing GRS [59], making the potential host harder to locate and parasitize.
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15 However, our logistic regressions suggest that bumblebee species with a large geographic
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17 range may be less often parasitized than species with a medium-sized distribution. This
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19 indicates that some species with large GRS are not attacked by brood parasites. There are
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21 several mutually non-exclusive explanations for why hosts with larger range sizes would not
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23 have brood parasites. It is possible that certain species with large GRS have had parasites, but
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25 for some reason have lost them, possibly because a widely-distributed host is a superior
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27 competitor against potential brood parasites species and is often better adapted to fight
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29 against parasites. This may be supported by the fact that reproduction by inquiline queens
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31 have been observed in the nests of only 24 out of 34 of host bumblebee species, while
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33 successful reproduction remains to be confirmed in 10 host species [32]. Analogous examples
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35 have also been found in birds and their brood parasites [60]. However, it is also possible that
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37 in some cases the existing parasitism has not been confirmed due to low parasite prevalence,
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39 which might be the case with the 10 bumblebee species with observations of non-reproducing
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41 *Psithyrus* queens in their nests. Evidently, more studies are needed to confirm the status of
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43 such inquiline–possible host species pairs.
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52 Conservation biology of parasites is challenging, because observing parasite species is always
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54 more difficult than observing their hosts. In general, parasitism depends on host GRS [61],
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56 and seems to be lower near the edges of host geographic ranges [61]. Therefore, the GRS of
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58 parasites tends to be smaller than those of their hosts [15]. Under this assumption, we
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3 developed a method to evaluate whether a given parasite species is likely to be lost from its
4 current host species, based on the GRS of both current and potential host species. We found
5 that several bumblebee species will probably lose their parasite species in the future. In this
6 respect, our results support observations of a general decline of bumblebee species and their
7 social brood parasites in North America [3,33,62] and Europe [8,15,33]. We also found that
8 relatively few parasite species have the potential to find a new suitable host that is closely
9 related to their current host (sectors A and B in Fig. 7). On the other hand, most host species
10 seem to have a high risk of losing their parasite species (sector C in Fig. 7). Those host
11 species should be a high priority for conservation efforts, as otherwise both the bumblebees
12 and their social parasite species will be lost [8]. Finally, we found that there are probably
13 several bumblebee species that have cuckoo bumblebee parasites that have not yet been
14 discovered (Table 4). To date, the hosts of less than half of the known cuckoo bumblebee
15 species have been confirmed [32]. Evidently, identifying the host species of cuckoo
16 bumblebees is vitally important for evaluating their conservation priorities; in Table 5, we
17 have listed bumblebee species that probably act as hosts of cuckoo bumblebees with still-
18 unknown hosts.

5. Conclusions

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48 To conclude, parasites are more vulnerable to extinction than are their hosts [8,63], and this
49 seems to be true also for social brood parasites. Human-induced environmental changes and
50 global warming will cause declines in the population sizes of hosts as well as in ranges of
51 brood parasites, because the probability of host shifts decreases. Our results highlight the fact
52 that the risk of extinction is highest in brood parasites that rely on rare or threatened host
53 species [8]. Thus, to lower the risk of extinction of brood parasite species, it is important to
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3 conserve their current hosts, especially in cases in which suitable closely related hosts do not
4 exist or have restricted geographic ranges. Our results show that GRS of host species can be
5 used to estimate the extinction risk of brood parasites, especially if information on
6 phylogenetic relationships among actual and potential hosts is available. However, long-term
7 datasets and more up-to-date information from larger geographical areas are required to
8 provide more insightful data in order to understand the proximate and ultimate reasons for the
9 risks of extinction of hosts and their social brood parasites.
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21 Acknowledgements

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26 We thank H. Hines for kindly providing the *Bombus* chronogram used in our analyses. We
27 thank also Jenni Kauppi and Sylvia Suhonen, who helped us in datamining and estimating
28 species-specific geographic range sizes from distribution maps.
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35 Ethics. No ethical problems. Ecological data and information on phylogenetic relationships in
36 this study were compiled based on a literature survey, see cited publications.
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42 Data accessibility. All relevant data are within the paper. Ecological data and information on
43 phylogenetic relationships in this study were compiled based on a literature survey, see cited
44 publications.
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51 Authors' Contributions. JSu and JSo collected data and designed the study. JSu coordinated
52 the study and compiled the database. JSu, TN and JJI conducted statistical tests and
53 phylogenetic analyses. All the authors contributed to manuscript preparation. All the authors
54 read and approved the final manuscript.
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5 Competing Interests. We have no competing interest.
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10 Funding. No financial support
11
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For Review Only

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Table 1. Estimated phylogenetic signals for the presence or absence of social brood parasitism (measured using the D statistic) and numbers of associated parasite species and geographic range sizes (GRS) (measured using Pagel's λ) in the three focal hymenopteran groups. N denotes the number of species in each host phylogeny, p values are given for deviations from absence of phylogenetic signal ($D = 1$, $\lambda = 0$) and from pure Brownian-model evolution ($D = 0$). In the case of bumblebees, phylogenetic signal is estimated for a full dataset of parasitized hosts ($n = 34$ cuckoo bumblebee species) and for hosts with observations of breeding cuckoo bumblebee queens ("Breeding queen") ($n = 24$ cuckoo bumblebee species).

Taxon and trait	N	D	p (D=0)	p (D=1)	λ	p ($\lambda=0$)
Bumblebees						
Parasitism	182	0.747	<0.001	0.028		
Breeding queen	182	0.976	<0.001	0.456		
Number of parasite species	182				0.015	0.910
GRS	182				0.292	0.004
Ants						
Parasitism	63	0.491	0.189	0.052		
Number of parasite species	63				0.266	0.064
GRS	63				0.243	0.227
Wasps						
Parasitism	37	1.16	<0.001	0.715		
Number of parasite species	37				0.001	0.999

Table 2. Results from analyses in which the presence of social parasites in bumblebees and *Myrmica* ants is modeled using logistic regression (all species as independent observations, 229 bumblebee species and 63 *Myrmica* ant species) and phylogenetic logistic regressions (182 bumblebee species and 63 *Myrmica* ant species). Two different models were used for bumblebees: one with every species known to host parasites (“All parasitism“, 34 cuckoo bumblebee species) and one including only host species where breeding cuckoo bumblebee queens have been observed (“Breeding queen“, 24 cuckoo bumblebee species). Explanatory variables were geographical range size (GRS, number of 611 000 km² grids) and GRS squared (GRS²). If GRS² was not statistically significant, only the model with GRS is presented.

Variable	Logistic regression				Phylogenetic logistic regression			
	Estimate	SE	Wald	P	Estimate	SE	t	P
Bumblebees								
<i>All parasitism</i>								
Intercept	-5.213	0.739	49.78	<0.001	0.008	0.446	0.02	0.985
GRS	0.272	0.052	27.60	<0.001	0.012	0.002	6.57	<0.001
GRS ²	-0.003	0.001	17.16	<0.001				
<i>Breeding queen</i>								
Intercept	-5.525	0.873	40.08	<0.001	0.014	0.438	0.03	0.974
GRS	0.249	0.058	18.49	<0.001	0.010	0.053	4.72	<0.001
GRS ²	-0.003	0.001	11.02	0.001				
<i>Myrmica</i> ants								
Intercept	-2.727	0.607	20.199	<0.001	0.072	0.242	0.30	0.766
GRS	0.105	0.043	5.960	0.015	0.009	0.005	1.85	0.069

Table 3. Bumblebee species that are likely to be parasitized or to have lost their social parasite, and the geographic area or a specific social parasite species that is a potential parasite for a given host species. The probability was calculated using non-phylogenetic logistic regression that was based on the geographic range size of current and potential hosts (see Fig 5a, Table 1). "GR" indicates the geographical region of each species.

<i>Bombus</i> species	Probability	GR	
Likely parasitized	%		Potential parasite species
<i>B. consobrinus</i>	63	Palaearctic	<i>B. barbutellus</i>
<i>B. cryptarum</i>	80	Holarctic	<i>B. bohemicus</i> , <i>B. vestalisi</i>
<i>B. cullumanus</i>	56	Palaearctic	Western Palaearctic species
<i>B. distinguendus</i>	64	Holarctic	<i>B. barbutellus</i>
<i>B. frigidus</i>	51	Nearctic	Nearctic species
<i>B. hyperboreus</i>	52	Holarctic	Western Palaearctic species
<i>B. laesus</i>	66	Palaearctic	Western Palaearctic species
<i>B. mixtus</i>	51	Nearctic	<i>B. insularis</i> , Nearctic species
<i>B. patagiatus</i>	53	Palaearctic	Western Palaearctic species
<i>B. schrencki</i>	66	Palaearctic	<i>B. rubestris</i> , <i>B. campestris</i>
<i>B. sporadicus</i>	65	Palaearctic	Western Palaearctic species
<i>B. subterraneus</i>	65	Palaearctic	<i>B. barbutellus</i>
<i>B. sylvicola</i>	63	Nearctic	<i>B. citrus</i> , Nearctic species
Likely lost parasite			Parasite species
<i>B. affinis</i>	7	Nearctic	<i>B. ashtoni</i>
<i>B. appositus</i>	7	Nearctic	<i>B. insularis</i> , <i>B. flavidus</i>
<i>B. argillaceus</i>	21	Palaearctic	<i>B. barbutellus</i>

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3	<i>B. bifarius</i>	21	Nearctic	<i>B. insularis</i>
4				
5	<i>B. bimaculatus</i>	12	Nearctic	<i>B. citrinus</i>
6				
7	<i>B. fervidus</i>	46	Nearctic	<i>B. insularis</i>
8				
9				
10	<i>B. flavifrons</i>	38	Nearctic	<i>B. insularis</i>
11				
12	<i>B. huntii</i>	18	Nearctic	<i>B. insularis</i>
13				
14	<i>B. hypnorum</i>	39	Palaearctic	<i>B. barbatellus, B. sylvestris</i>
15				
16	<i>B. impatiens</i>	18	Nearctic	<i>B. citrinus, B. insularis</i>
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18				
19	<i>B. jonellus</i>	31	Holarctic	<i>B. flavidus, B. quadricolor</i>
20				
21	<i>B. lapidarius</i>	49	Palaearctic,	<i>B. ruperstris</i>
22				
23	<i>B. monticola</i>	14	Palaearctic,	<i>B. sylvestris</i>
24				
25	<i>B. nevadensis</i>	18	Nearctic	<i>B. insularis</i>
26				
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28	<i>B. occidentalis</i>	29	Nearctic	<i>B. suckleyi, B. flavidus</i>
29				
30	<i>B. pascuorum</i>	42	Palaearctic	<i>B. campestris, B. rupestris</i>
31				
32	<i>B. pomorum</i>	24	Palaearctic	<i>B. campestris</i>
33				
34	<i>B. ruderatus</i>	24	Palaearctic	<i>B. inexpectatus, B. barbutellus</i>
35				
36	<i>B. rufocinctus</i>	44	Nearctic	<i>B. insularis, B. flavidus</i>
37				
38	<i>B. sylvarum</i>	46	Palaearctic	<i>B. campestris</i>
39				
40	<i>B. ternarius</i>	24	Nearctic	<i>B. insularis</i>
41				
42	<i>B. terricola</i>	49	Nearctic	<i>B. ashtoni</i>
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44	<i>B. vagans</i>	38	Nearctic	<i>B. citrinus</i>
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Figure legends

Figure 1. Conceptual description of the effects of phylogenetic relatedness, geographic range size (GRS) (assumed to correlate positively with overall population size), and similarity of ecological traits and chemical signatures on the probability of shifts among current and potential host species by social brood parasites. The P denotes a parasite species facing a decision of whether or not to shift onto a new host, and the size of arrows indicates host shift probabilities (HSP) onto different hosts. The consequences of realized shifts for phylogenetic signals are shown below the figures.

Figure 2. Phylogenetic tree of 182 eusocial bumblebee species, with bar plots showing species-specific geographic range sizes (measured as the number of 611 000 km² squares occupied) and numbers of associated social brood parasite species. In both plots, species attacked by parasites are indicated by black bars.

Figure 3. Phylogenetic tree of 63 eusocial *Myrmica* ant species, with bar plots showing species-specific geographic range sizes (measured as the number of 611 000 km² squares occupied) and numbers of associated social brood parasite species. Parasitized species are indicated by black bars.

Figure 4. Phylogenetic tree of 37 eusocial vespine and polistine wasp species, with bar plot showing numbers of associated social brood parasite species.

Figure 5. Probability (%) of the presence of social brood parasitism in (a) bumblebee species and (b) ant species in relation to species-specific geographic range size (number of 611 000 km² grids). In (a), the continuous line is based on all host species for which social brood parasites have been observed, whereas the dashed line is based only on cases in which a breeding queen of a social brood parasite has been observed [32]).

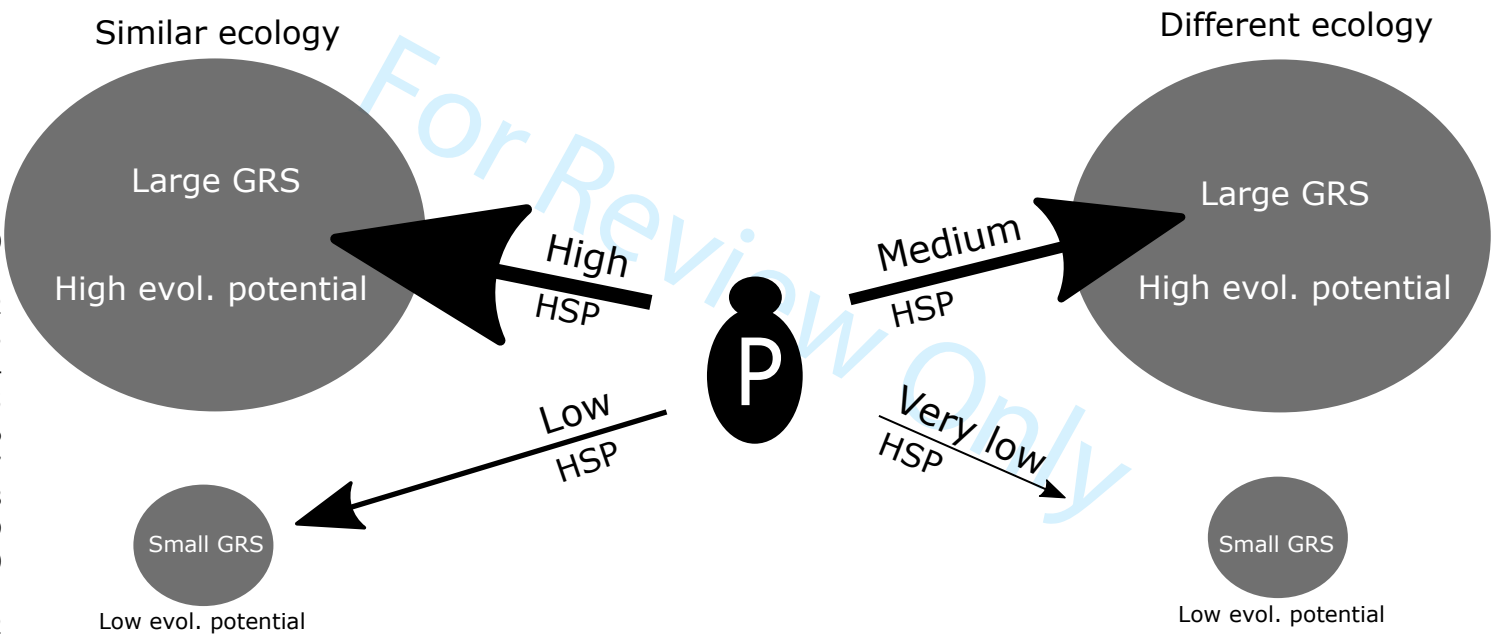
Figure 6. The geographic range size (number of 611 000 km² grids) of parasitized (a) bumblebee species and (b) *Myrmica* ant species plotted against the GRS of their most closely related unparasitized species. The continuous line indicates an equal GRS in host and non-host species. Below the line are species pairs in which the GRS of the parasitized species is larger than that of its closest unparasitized relative.

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5 Figure 7. Probability (%) of social parasitism of potential bumblebee host species in relation
6 to parasitized bumblebee host species. The continuous line indicates an equal probability
7 between host and non-host species. The symbols below the continuous line represent a
8 situation where the most closely related unparasitized species has a smaller probability than
9 the parasitized bumblebee host species. Dotted lines indicate a 50 % probability of infection.
10 Species in sector A) are likely to have lost their social parasite but have an alternative closely
11 related potential host, in B) have a social parasite and have also a closely related potential
12 host, in C) have lost their social parasite and do not have a closely related potential host, and
13 in D) have a social parasite, but do not have a closely related potential host.
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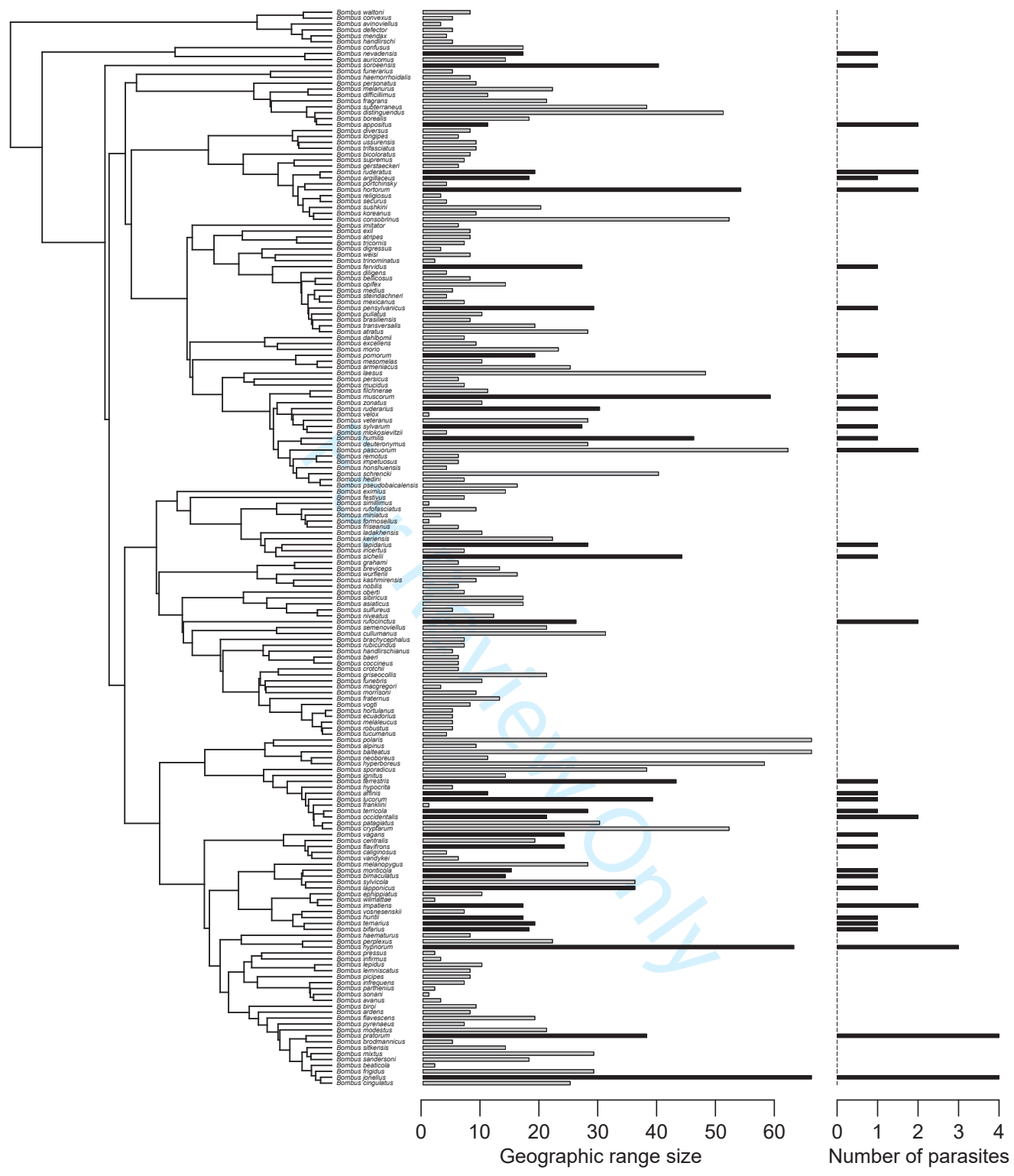
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Closely related species

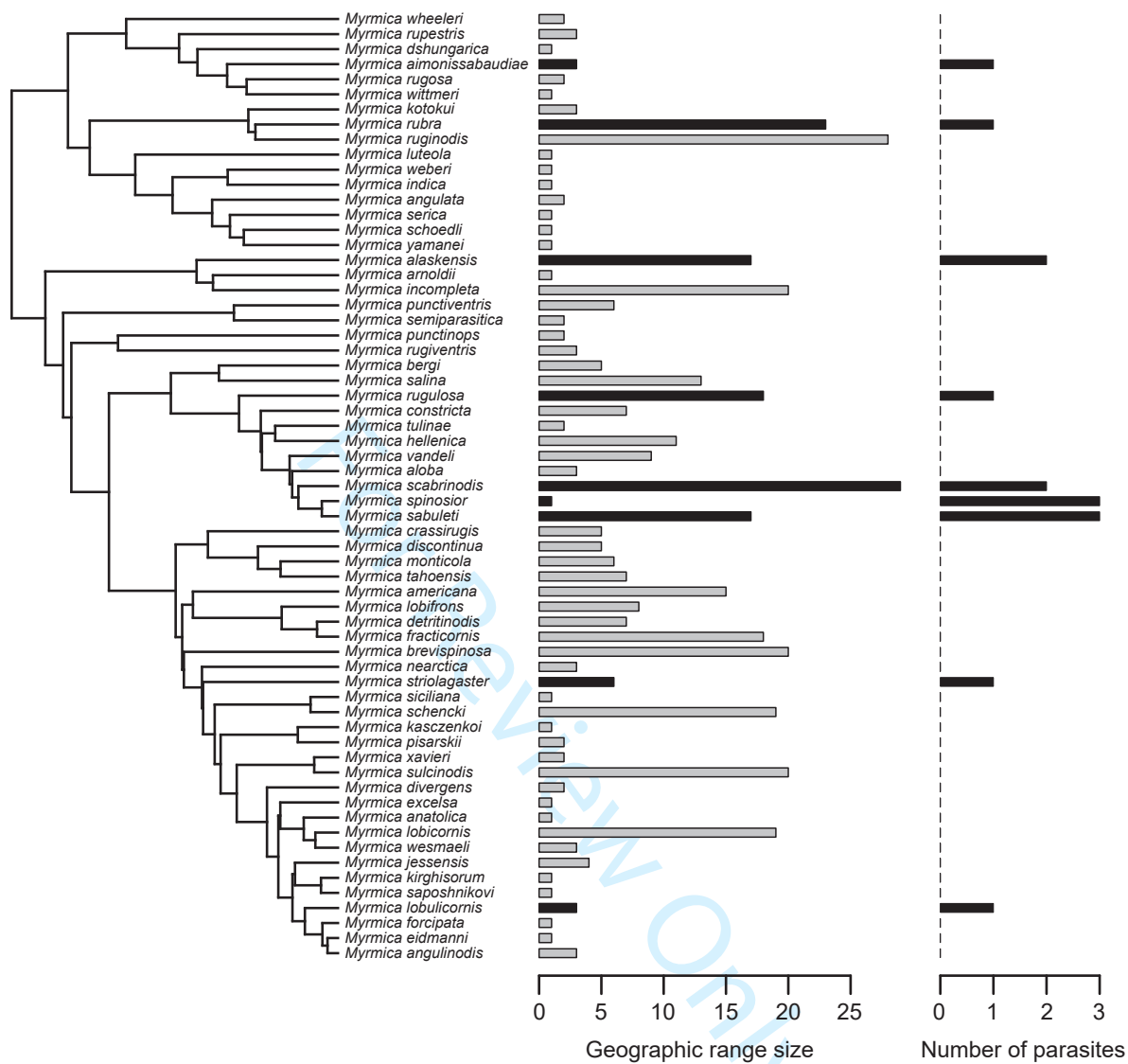
Distantly related species



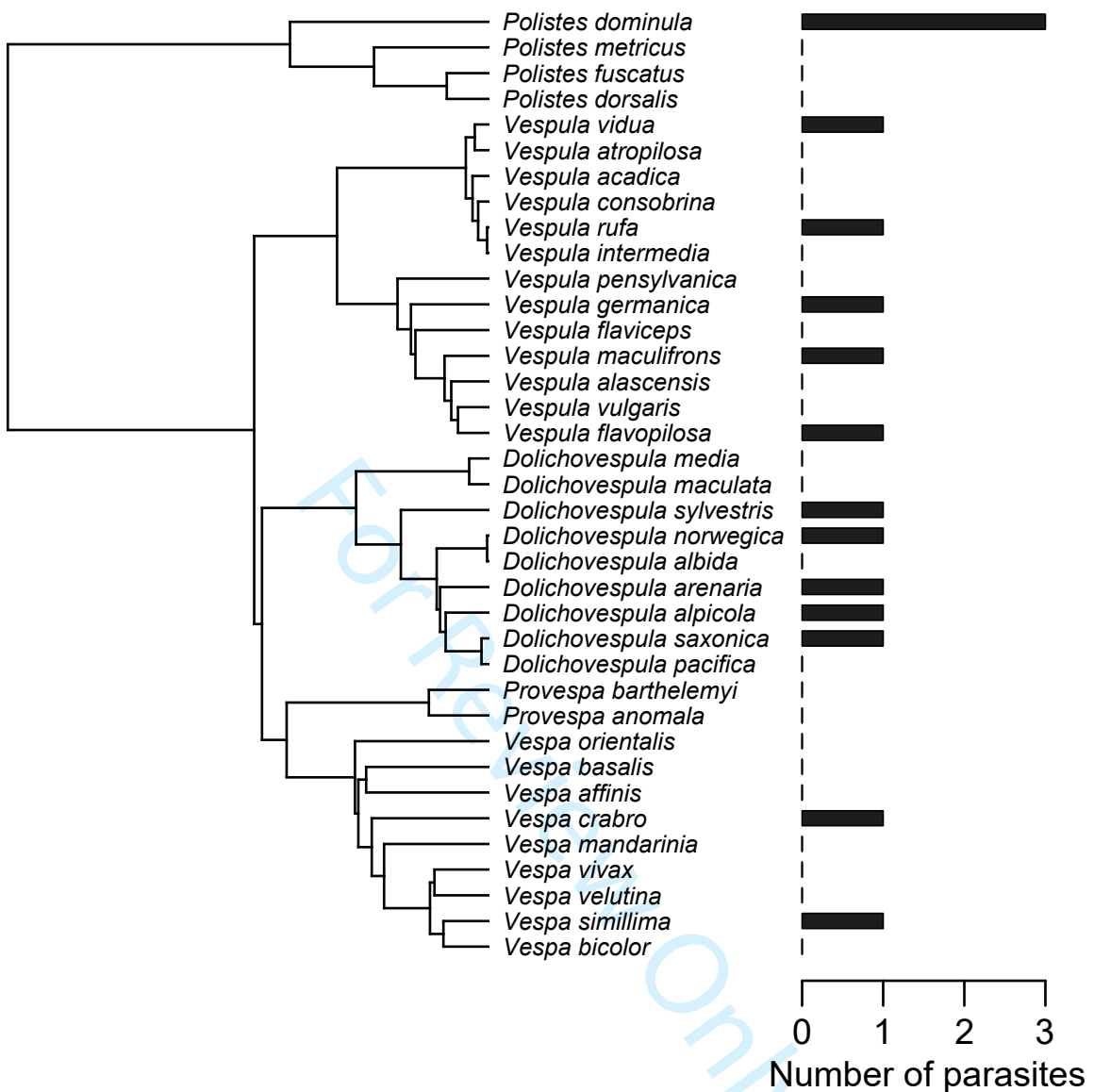
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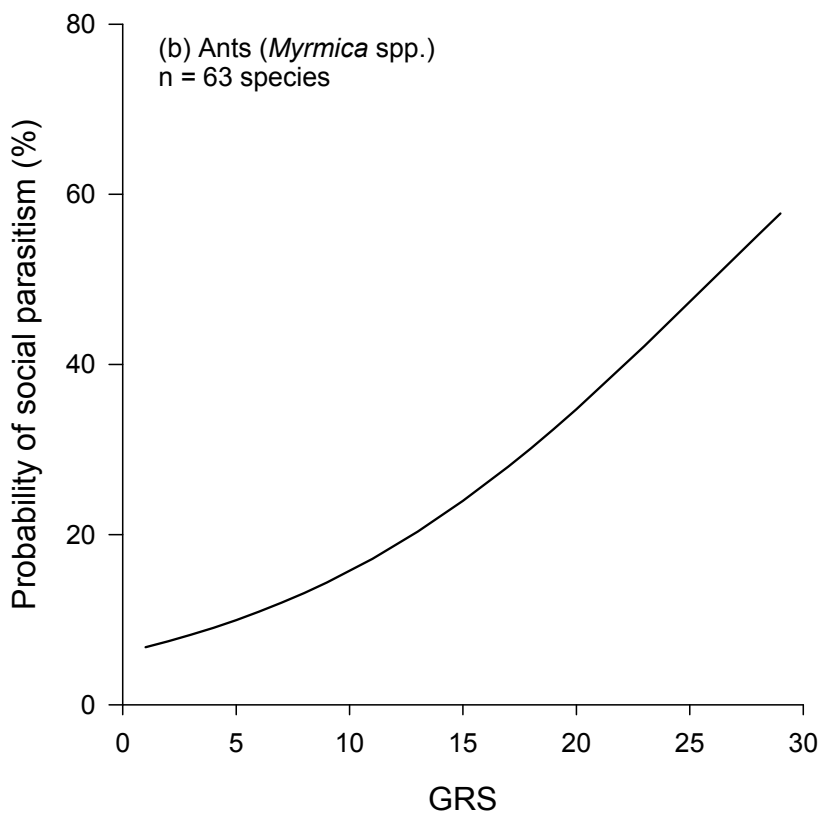
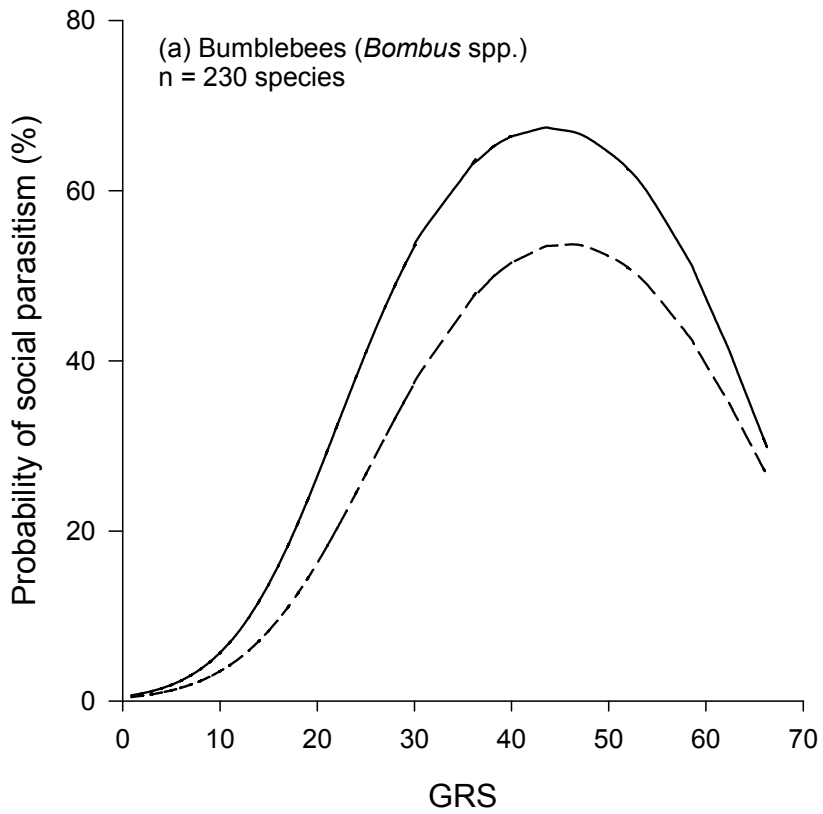
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