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► To cite this version:

Olli Loukola, Peter Adamik, Frank Adriaensen, Emilio Barba, Blandine Doligez, et al.. The roles of temperature, nest predators and information parasites for geographical variation in egg covering behaviour of tits (Paridae). *Journal of Biogeography*, 2020, 47 (7), pp.1482-1493. 10.1111/jbi.13830 . hal-02990542

HAL Id: hal-02990542

<https://cnrs.hal.science/hal-02990542v1>

Submitted on 19 Nov 2020

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1 The roles of temperature, nest predators and information parasites
2 for geographical variation in egg covering behaviour of tits
3 (Paridae)

4
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20 The dataset supporting this article will be available from the Dryad Digital Repository

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1 Abstract

2

3 **Aim** Nest building is widespread among animals. Nests may provide receptacles for
4 eggs, developing offspring and the parents, and protect them from adverse
5 environmental conditions. Nests may also indicate the quality of the territory and its
6 owner and can be considered as an extended phenotype of its builder(s). Nests may,
7 thus, function as a sexual and social signal. Here, we examined ecological and abiotic
8 factors – temperature, nest predation and interspecific information utilization – shaping
9 geographical variation in a specific nest structure - hair and feather cover of eggs – and
10 its function as an extended phenotype before incubation in great (*Parus major*) and blue
11 tits (*Cyanistes caeruleus*) across Europe. We also tested whether egg covering is
12 associated with reproductive success of great tits.

13 **Location** 14 different study sites and 28 populations across Europe.

14 **Methods** We recorded clutch coverage estimates and collected egg covering nest
15 material from the tit nests. We also measured nest specific breeding parameters and
16 phenotypic measurements on adults. We tested whether mean spring temperatures, nest
17 predation rates and flycatcher (*Ficedula* spp) densities in the study areas explain the
18 large-scale geographical variation of clutch coverage and reproductive success of tits.

19 **Results** The degree of egg coverage of great tits increased with lower mean spring
20 temperature, higher nest predation rate and higher flycatcher density. We did not find
21 egg covering of blue tits to be associated with any of the ecological or abiotic factors.
22 Moreover, egg covering of great tits was not associated with reproductive success in our
23 cross-sectional data, yet a rigorous assessment of fitness effects would require long-term
24 data.

1

2 **Main conclusions** Our findings suggest that, in great tits, egg covering may
3 simultaneously provide thermal insulation against cold temperatures during egg-laying
4 in spring and also represent a counter-adaptation to reduce information parasitism by
5 flycatchers and nest predation. Hence, geographical variation in interspecific
6 interactions, and consequently in coevolutionary processes, may affect the evolution of
7 nest characteristics besides environmental conditions.

8

9 **Keywords**

10 Bird nest, breeding success, *Cyanistes caeruleus*, extended phenotype, nest structure,
11 *Parus major*.

12

1. Introduction

In the animal kingdom, nest-building is a common behaviour. The basic functions of nest-building are thought to be protection against elements of abiotic (e.g., low temperatures, humidity) and biotic (e.g., nest predators, parasites) risks for offspring until they hatch or become independent from parental care (Hansell, 2007). Nest structure shows large variation across species. Some species invest a considerable amount of time and resources in building complex and decorated nest structures while, in others, just a few pieces of rock or plant material are enough (Hansell, 2007). This implies that nests may also have functions other than offering security to offspring during development. In some species, such as the stickleback (*Gasterosteus aculeatus*) (Barber et al., 2001; Östlund-Nilsson & Holmlund, 2003), cichlid fishes (McKaye et al., 1990; Schaedelin & Taborsky, 2006) and passerines (Grubbauer & Hoi, 1996; Hoi et al., 1994; Jelínek et al., 2016), the nest has become a signal in mate attraction and selection (Schaedelin & Taborsky, 2009). In black kites (*Milvus migrans*), the decoration of nests with pieces of white plastic is a reliable signal in dominance hierarchy among conspecifics (Sergio et al., 2011). Thus, a perceptible nest can be considered an extended phenotype of its builder(s) (Dawkins, 2016), because the placement, structure, materials, and size of the nest affects the probability that the genes of the builder(s) are transmitted to the next generation by affecting mate selection and offspring survival probability.

Extended phenotypes, such as odour, chemical marks, nests and other constructions (webs, excavations, burrows, bowers, piles or pieces of various materials), are often important signals in intentional communication among conspecifics related to mate attraction and selection, dominance hierarchy, territory defence, and species recognition

1 (Schaedelin & Taborsky, 2009). These signals may also be long-lasting and readily
2 available to heterospecifics, actually providing a source of inadvertent information
3 about the location, decisions, social structure and dominance, body condition, and
4 cognitive capabilities of signal producers to those who can interpret the signals. For
5 example, in bowerbirds (family Ptilonorhynchidae), the elaborateness of the display
6 structure, the bower, reflects the species identity and also the age and experience of the
7 focal male (Vellenga, 2016). Both con- and heterospecifics may thus use it to make
8 inferences about the quality of the territory and its owner.

9 The use of inadvertent information is common among conspecifics (Danchin et al.,
10 2004) but also among heterospecifics (Seppänen et al., 2007). Most valuable
11 interspecific information is predicted to be provided by species with overlapping
12 resource needs (Seppänen et al., 2007). Many traits defining extended phenotypes have
13 been shown or suggested to be used by heterospecifics as sources of information: tit
14 (Paridae) clutch size by flycatchers (*Ficedula* spp) for breeding habitat selection
15 (Forsman & Seppänen, 2011; Loukola, Seppänen, Krams, Torvinen, & Forsman, 2013;
16 Samplonius, Kappers, Brands, & Both, 2016; Seppänen & Forsman, 2007; Seppänen,
17 Forsman, Mönkkönen, Krams, & Salmi, 2011), sibling vole's (*Microtus*
18 *rossiameridionalis*) odour and chemical signals by field voles (*M. agrestis*) for predator
19 avoidance (Hughes et al., 2010) and stingless bee's (*Melipona rufiventris*) odour and
20 chemical signals by another stingless bee species (*Trigona spinipes*) for space use and
21 foraging decisions (Nieh et al., 2004). However, in contrast to bodily phenotypes, we
22 know very little about geographic variation of extended phenotypes (but see Deeming &
23 Mainwaring, 2015; Hansell, 2000) and the potential processes behind the patterns.

1 Tits' distribution ranges are large, and thus, their nesting behaviours provide a good
2 model system to examine large-scale geographic patterns of extended phenotypes. All
3 tit species are cavity nesting, and the basic structure of the nest consists of moss and a
4 layer of animal hair or feathers on top, on which eggs are laid. During egg-laying, eggs
5 are usually covered with a loose tuft of hair, feathers, moss, hay or other light material.
6 This characteristic, the covering of eggs, is our trait of interest because it occurs widely
7 in genus *Parus* and *Cyanistes* (Haftorn & Slagsvold, 1995), yet the propensity to cover
8 the eggs varies both among individuals within populations and among geographically
9 distinct populations (Loukola et al., 2014). In great tits, usually all eggs are totally
10 covered with hair, but sometimes the cover is partial or does not exist at all (Loukola et
11 al., 2013).

12 Three mutually non-exclusive hypotheses have been put forward to explain great and
13 blue tit nest structure and egg covering behaviour (Haftorn & Slagsvold, 1995). First,
14 *the insulation hypothesis* predicts that the cover provides thermal insulation against cold
15 temperatures during egg-laying in spring. Indeed, recent studies show that the mass and
16 insulation capacity of great and blue tit nests are lower at high ambient temperature
17 (Deeming, Mainwaring, Hartley, & Reynolds, 2012; Mainwaring et al., 2014).

18 Secondly, *the nest predation hypothesis* postulates that egg covering is a protection
19 against nest predators (Haftorn & Slagsvold, 1995; Saavedra & Amo, 2019) or
20 interspecific competitors that may damage the nest. For example, recent experiment by
21 Saavedra & Amo (2019) showed that blue tits covered their eggs more frequently when
22 they detected an increase in the perceived risk of predation. Kreisinger and Albrecht
23 (2008) showed experimentally that mallard (*Anas platyrhynchos*) nests that were
24 covered with nest material, suffered significantly lower rates of nest predation than

1 nests which were left uncovered. An example of the interspecific competition is found
2 in house wrens (*Troglodytes aedon*) in North America that may destroy the nests of
3 black-capped chickadees (*Poecile atricapillus*) and tufted titmice (*Baeolophus bicolor*)
4 (White & Kennedy, 1997). In general, nest predation is a major factor affecting the
5 behaviour and life-history traits in birds (Martin & Briskie, 2009).

6 Finally, the most recent hypothesis, *the information parasitism hypothesis*, suggests that
7 great tits cover eggs to protect against information acquisition by flycatchers (Loukola
8 et al., 2014). Upon arrival, migratory flycatchers are attracted to the proximity of
9 resident tits during their nest-site selection that results in fitness benefits (Forsman,
10 Seppänen, & Mönkkönen, 2002) and the visible clutch size of tits seems to be an
11 important source of information for flycatchers. In general, the tits are still in egg laying
12 stage when the Flycatchers prospect tits' nests in spring (Forsman et al., 2018; Forsman
13 & Thomson, 2008; Samplonius & Both, 2019) and may use tit clutch size to adjust their
14 own investment in the offspring (clutch size and egg mass) (Forsman, Seppänen, &
15 Nykänen, 2011), and in deciding whether they would copy or reject nest-site
16 preferences of the focal tits (Forsman & Seppänen, 2011; Loukola et al., 2013;
17 Seppänen et al., 2011). Flycatchers' interest in the clutch size of tits makes sense as
18 environmental variation explains a large amount of variance in clutch size in blue tits
19 (e.g. Tremblay, Thomas, Lambrechts, Blondel, & Perret, 2003) and great tits (e.g.
20 Beldal et al., 1998), implying that tit clutch size reliably reflects the quality of the
21 environment and/or parents and can readily be used as a cue on territory quality. Thus,
22 tit nests can be considered to include two components of an extended phenotype that are
23 used by information parasites: clutch size (reflecting parental/territorial quality) and nest
24 structure that covers the clutch totally, partially or not at all.

1 The information utilization by flycatchers is not neutral to tits. The selective copying of
2 nest-site characteristics by flycatchers may lead to niche convergence (Loukola et al.,
3 2013) and result in fitness losses in great tits in terms of the number and condition of
4 fledglings (Forsman, Thomson, & Seppänen, 2007). Once flycatchers (i.e. the
5 information parasite) have evolved a strategy for taking advantage of a tit (i.e. the host),
6 tits are expected to evolve counter-adaptations, which may lead to an evolutionary arms
7 race (Dawkins & Krebs, 1979) between the tits and the flycatchers on acquiring and
8 hiding information (Seppänen et al., 2007). Indeed, a recent study by Loukola et al.
9 (2014) experimentally demonstrated that the simulated presence of pied flycatchers
10 increased the amount of hair great tits brought on the eggs and covered them more
11 carefully when exposed to flycatcher playback song compared to the control treatment
12 with a playback song of a non-information-parasitic species. Thus, great tits' nest
13 structure and covering eggs with hair may also be a counter-adaptation to reduce
14 information parasitism.

15 Phenotypes (bodily and extended) often show geographic variation suggesting spatial
16 variation in selection regimes (Mayr, 1956; Slatkin, 1973). The nests of birds make no
17 exception (Deeming & Mainwaring, 2015; Hansell, 2000). Comparing egg covering
18 behaviour of great and blue tits among different populations at a large geographical
19 scale facilitates testing the insulation, nest predation and information parasitism
20 hypotheses. This is because each of temperature during egg-laying period, the
21 abundance of nest predators and potential information parasites (flycatchers) of tits vary
22 geographically. As we do not know whether the hypothesized mechanisms have
23 additive or interactive effects on egg covering behaviour, we test our hypotheses based
24 on these perspectives; if the insulation, nest predation and information parasitism have

1 additive effects on egg covering behaviour, the extent of egg covering should increase
2 with lower mean spring temperature and higher nest predation rate. Based on results of
3 Loukola et al. (2014), we also predict an increased extent of egg covering in the
4 presence and density of potential information parasites. If there is an interactive
5 component in how the hypothesized mechanisms affect egg covering behaviour,
6 interactions among mean spring temperature, nest predation rate and density of
7 information parasites should be found in statistical analysis.

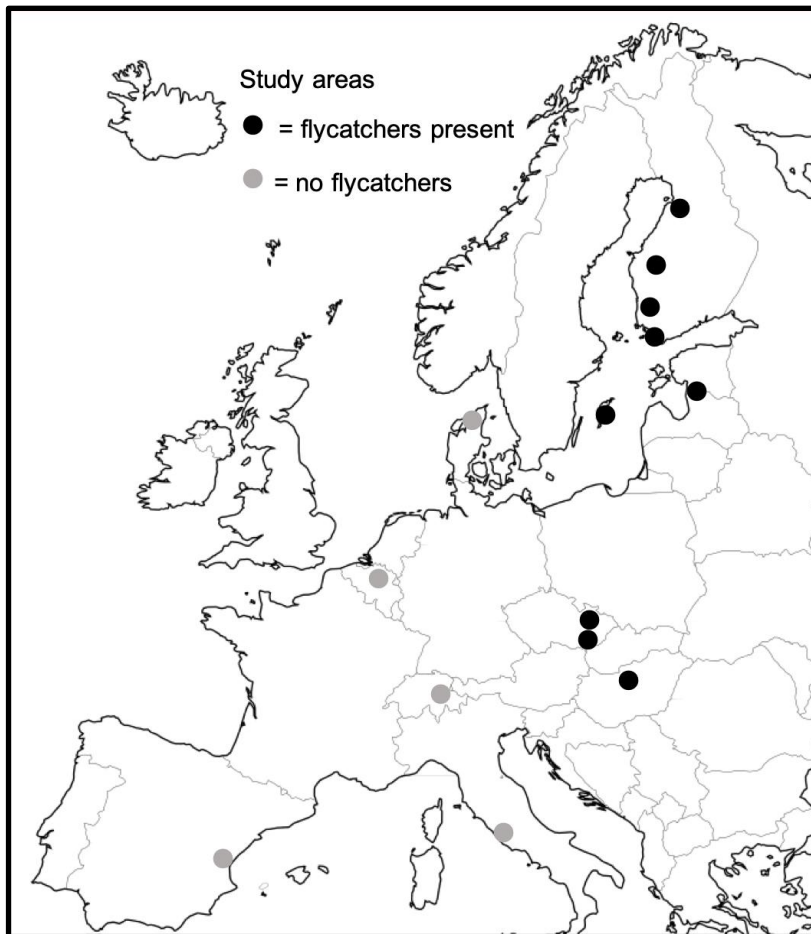
8 In addition to main hypotheses, other variables, such as nest floor area and habitat type,
9 may affect tits egg covering behaviour. Tits establish the fully lined nest cup only at the
10 start of incubation (Deeming, Morton, & Laverack, 2019). If the eggs are spread out
11 over a wider area in nest boxes with larger floor area, we expect that more material is
12 needed to cover the eggs. If the density and the species composition of local bird and
13 mammal communities, which are linked to various characteristics of the habitat,
14 including tree species, affect the availability of feathers and hairs (egg covering
15 material), we expect to find differences in the extent of egg covering in study sites with
16 different habitat types. Finally, we explore whether reproductive success of the tits
17 (number of hatched eggs and fledglings) is positively associated with extent of egg
18 covering, as would be expected if egg covering behaviour is under positive natural
19 selection.

20 **2. Methods**

21 **(a) Study areas**

22 The great tit data for this study were collected in spring 2013 from 10 different
23 countries, 14 study areas (Figure 1, Table S1) and 28 populations in Europe. The blue tit

1 data were collected in the same year from six out of the 10 countries, eight out of the 14
2 study areas and 22 out of the 28 populations. All study populations breed in nest boxes.
3 Research was carried out in accordance with legislation of each country.



5 **Figure 1. A map of Europe showing the locations of the study areas. See**
6 **Supplementary table S1 for more details concerning the study populations.**

7 **(b) Field procedure**

8 Nest building state and the beginning of the egg laying (laydate) were checked during
9 regular field observations. Use of egg cover tends to increase during the first days of the
10 laying stage (Haftorn & Slagsvold, 1995). During the egg-laying stage, when tits had
11 laid their 4th – 6th egg, (1) the nest was photographed to get a measurement of the extent

1 of the clutch coverage, i.e. the proportion of the visible clutch surface (%) and (2) all the
2 hair and other material that covered tit eggs and nest cup was removed to expose the
3 eggs and placed in a zip lock bag for later measurement of hair mass and the nest was
4 photographed again. After photographing the nest, the removed material was replaced
5 by same quantity of sheep hair. The onset of incubation was determined by observing
6 the presence of female on the nest and touching eggs to determine whether the eggs
7 were cold or warm. Nest specific breeding parameters (number of hatched eggs and
8 fledglings) and phenotypic measurements on adults (Table 1) were also collected. We
9 recorded clutch coverage estimates and mean spring temperatures (from the nearest
10 available meteorological stations to each of the study area) from 476 great tit nests and
11 123 blue tit nests and nest predation rates from 345 great tit nests and 74 blue tit nests.
12 Flycatcher (either *F. hypoleuca* or *F. albicollis*) density was measured in the end of
13 breeding season as the proportion of nest boxes occupied by flycatchers in the study
14 population.

15 **(c) Measurement of nest characteristics**

16 The clutch coverage rate was measured by comparing the proportions of the visible
17 clutch surfaces from the digital photographs taken from the nest before and after cover
18 removals using ImageJ software (US National Institutes of health,
19 <http://imagej.nih.gov/ij>). The clutch surface was measured using freehand tracing and
20 area calculator tools. Clutch surfaces were measured twice from each picture to
21 minimize measurement error and average values were used in the analyses. Masses of
22 the collected hair samples were weighed to the nearest 0.0001 g by using an Ohaus
23 AS120S analytical balance. Phenotypic measurements on adult tits were obtained when
24 they were captured during food provisioning. Age was classified in the field as one-

1 year-old (second calendar year) or older (at least third calendar year) (Jenni & Winkler,
 2 1994). Adult and young birds were handled under the ringing licenses of the authors.
 3 Hence, our study complied with the national legislation of Belgium, Czech Republic,
 4 Denmark, Estonia, Finland, Hungary, Italy, Spain, Sweden and Switzerland concerning
 5 handling wild animals. Variables used in statistical analyses are listed in Table 1.

6 **Table 1. List of variables. Model sets refer to the different sets of models that**
 7 **were used in assessing the study hypotheses (see Statistical methods section**
 8 **for details).**

Name of the variable	Model set	Type of the variable	Definition of the variable
Clutch coverage	1 – 5, 10 6 – 9	Response Explanatory	First principal component of clutch covering rate and the mass of the covering material
Number of hatched eggs	6, 7	Response	
Number of fledglings	8, 9	Response	
Dominant tree genus in the study area	1 – 5, 10	Explanatory	Defines the habitat type. Affects egg covering material availability
Age of the tit parent(s)	6 – 9	Explanatory	Binary variable; one-year-old or older
Flycatcher density	1 – 9	Explanatory	Proportion of nest boxes occupied by flycatchers in the study area. Standardized in model sets 6 – 9
Flycatcher presence	10	Explanatory	Binary variable; flycatcher present or not
Mean spring temperature	1 – 9, 10	Explanatory	Mean daily temperatures (°C) between the beginning of the nest building and fledging, from the nearest available meteorological stations to each of the study area. Standardized in model sets 6 – 9
Clutch size	6 – 9	Explanatory	Final number of eggs in the nest
Nest predation rate	1 – 10	Explanatory	The proportion of predated nests within a study site. Standardized in model sets 6 – 9. Nests where devices had been added to prevent nest predation (e.g. wire netting) were removed from the analysis
Study population	1 – 5, 10	Random factor	
Nest floor surface	1 – 5, 10	Explanatory	Surface area of the nest box floor in cm ² . Standardized in model sets 4 and 5
Geographical location	1 – 5, 10	Explanatory	First principal component of altitude, latitude and longitude

9

10

1 (c) Statistical methods

2 The distribution of clutch covering rate (proportion of covered eggs) was slightly U-
3 shaped with a high peak at one (all eggs covered), which is problematic for analysis.
4 Therefore, we measured clutch coverage by combining clutch covering rate and the
5 mass of material used to cover the eggs, because these variables together measure the
6 investment of the tit parents in covering their clutch. For this purpose, we ran principal
7 component analysis for the data on egg coverage and the mass of the covering material
8 and used the first principal component ('clutch coverage' hereafter, explains 72.3 % of
9 the variance, eigenvalue = 1.0) as a response variable when analysing variation in clutch
10 covering behaviour. Clutch coverage variable was symmetrically (approximately
11 normally) distributed, and positively correlated with both clutch covering rate and mass
12 of the covering material, higher values, thus, indicating higher investment in clutch
13 covering (Supplementary figure S1).

14 All statistical analyses were conducted with R version 3.4.3 (R Core Team, 2017).
15 Linear mixed-effects models (LMMs; function 'lme' in package nlme (Pinheiro et al.,
16 2017)) were used to analyse variation in the clutch covering of great (Model sets 1 – 4)
17 and blue tits (Model set 5). Generalized linear mixed-effects models (GLMMs; function
18 'glmer' in package lme4 (Bates et al., 2014)) with Poisson distribution and a
19 logarithmic link function were used to analyse variation in the number of hatched eggs
20 and fledglings of the great tits (Model sets 6 – 9). In model sets 6 – 9, we standardized
21 all continuous explanatory variables of the model. Standardization makes the
22 quantitative interpretation of model parameters less intuitive, which is the reason why
23 standardization was used only when it was really needed for aiding/facilitating model
24 convergence. We used multi-model inference; effects of analysed variables were

1 summarized by model averaging (Burnham & Anderson, 2002)) (function ‘model.avg’
2 in package MuMIn (Barton, 2009)).

3 We derived ten model sets. **Model set 1** (Table 2a) tested if the alternative hypotheses
4 (i.e. insulation, nest predation, information parasitism), nest floor surface area or forest
5 type (dominant tree genus) in the study site explain variation in clutch coverage in great
6 tits. This model set was fitted to data ($N_{\text{observations}} = 341$) including observations from all
7 the study sites, also including sites where the flycatcher density was zero. Mean spring
8 temperature, nest predation rate, flycatcher density, nest floor surface area, first
9 principal component of geographical variables (altitude, latitude and longitude) and
10 dominant tree genus in the study site were set as fixed effects, and population as a
11 random effect in the global model. Time of the year (Laydate) was not included in the
12 analysis because it is strongly negatively correlated with the first principal component
13 of geographical variables (Pearson’s correlation, $r = -0.61$, $t = -3.41$, $df = 343$, $p\text{-value} <$
14 0.001) (see Laydate in Supplementary table S3). Nest predation rate positively
15 correlates with mean spring temperature ($r = 0.67$) but both of these variables were
16 retained in all models because of their importance for assessing the study hypotheses.
17 No interactions were included in any model. The set of all meaningful models simpler
18 than the global model was derived with the function ‘dredge’ (package ‘MuMIn’
19 (Bartón & Barton, 2017)) for model averaging, the global model being included in
20 model averaging (see Supplementary table S2a for the set of averaged models).
21 Bivariate correlations between the study variables are provided in Supplementary
22 materials (Supplementary table S3).

23 **Model set 2** (Table 2b) was derived otherwise similarly to model set 1, but all possible
24 interactions among the nest predation rate, mean spring temperature and flycatcher

1 density were included in the global model (see Supplementary table S2b for the set of
2 averaged models).

3 **Model set 3** (Table 3a) was derived otherwise similarly to model set 1, but these models
4 were fitted to data including only areas where the flycatchers were present (flycatcher
5 density > 0, $N_{\text{observations}} = 169$, see Supplementary table S4a for the set of averaged
6 models). This was done to reliably estimate the effect of flycatcher density. In the full
7 data the high number of zeros (flycatchers not present) might confound the estimation
8 (underestimation) of flycatcher density effect on great tit egg-covering behaviour.

9 **Model set 4** (Table 3b) was derived otherwise similarly to model set 3, but all two-way
10 interactions among the nest predation rate, mean spring temperature and flycatcher
11 density were included in the global model (the three-way interaction was ignored as the
12 model-fitting failed when it was included in the global model; see Supplementary table
13 S4b for the set of averaged models).

14 **Model set 5** ($N_{\text{observations}} = 74$; Supplementary table S5) was otherwise similar to model
15 set 1, but it focused on variation in clutch coverage in blue tits (see Supplementary table
16 S6 for the set of averaged models). Because of the low number of blue tit observations,
17 we did not conduct any further analyses for this species.

18 **Model sets 6 and 7** tested whether the clutch coverage of great tits or the ecological and
19 abiotic environment explain the number of hatched eggs of great tits by using all great
20 tit data.

21 In **model set 6** (Supplementary table S7), number of hatched eggs was used as a
22 dependent variable and clutch size was added as a covariate in the global model in both
23 model sets to take the effect of clutch size variation into account. In addition to clutch

1 size, fixed effects of the global models included also clutch coverage, mean spring
2 temperature, nest predation rate, flycatcher density, as well as female age and its
3 interaction with clutch size, because female age affects clutch size (Perrins & McCleery,
4 1985). Population was set as a random effect. Except clutch size (a non-negative
5 integer), continuous variables were standardized (by subtracting mean from each
6 observation and dividing this difference by standard deviation, see Supplementary table
7 S8 for the set of averaged models) to aid model convergence.

8 **Model set 7** (Supplementary table S9) was derived otherwise similarly to model set 6,
9 but all possible interactions among the nest predation rate, mean spring temperature and
10 flycatcher density were included in the global model (see Supplementary table S10 for
11 the set of averaged models).

12 **Model sets 8** (Supplementary table S11 (see Supplementary table S12, for the set of
13 averaged models)) **and 9** (Supplementary table S13 (see Supplementary tables S14, for
14 the set of averaged models)) tested whether the clutch coverage of tits or the ecological
15 and abiotic environment explain the number of fledged offspring of great tits and were
16 derived otherwise similarly to model sets 6 and 7, respectively, but number of fledged
17 offspring was used as a dependent variable. Population was set as a random effect in all
18 models.

19 **Model set 10** (Supplementary table S15 (see Supplementary table S16, for the set of
20 averaged models)) was otherwise similar to model set 1, but flycatcher density was
21 replaced with flycatcher presence (binary variable; flycatcher present or not) for
22 checking whether the results are sensitive to the way how flycatcher density is handled
23 (continuous vs. presence/absence).

3. Results

Model set 1 showed that clutch coverage of great tits was negatively associated with the mean spring temperature, positively associated with nest predation rate and nest floor surface area (Table 2a and Figure 2). Clutch coverage was also affected by the dominant tree genus, being particularly high at sites dominated by genus *Citrus* trees (Table 2a).

Model set 2 showed no evidence of any interactions among the hypothesized mechanisms affecting clutch coverage (Table 2b).

When focusing only on sites where flycatchers are present (model set 3), clutch coverage was positively associated with the flycatcher density (Figure 3), but the mean spring temperature and nest predation rate effects disappeared in this smaller subset of the data (Table 3a).

Model set 4 showed no evidence of any interactions among the hypothesized mechanisms affecting clutch coverage on sites where flycatchers are present (Table 3b).

Model set 5 showed that clutch coverage of blue tits was not associated with any of ecological or abiotic factors (Supplementary table S5).

Model sets 6 and 8 showed that both the numbers of hatched eggs and fledged offspring were positively associated with clutch size, as expected, and number of fledged offspring was positively associated with mean spring temperature, but neither of them was associated with clutch coverage, predation rate, flycatcher density or female age (Supplementary tables S7 and S11 and Supplementary figures S2 and S3).

Model sets 7 and 9 showed no evidence of any interactions among the hypothesized mechanisms affecting reproductive success (Supplementary tables S9 and S13).

1 Model set 10 showed that replacing the flycatcher density to flycatcher presence as an
2 explanatory variable did not change the model-averaged results (Supplementary table
3 S15).

4

1

2 **Table 2. Model-averaged (full average) fixed effects in model sets 1 and 2**
3 **explaining clutch coverage in the great tit. Model set 1 is based on the**
4 **assumption that temperature, nest predation and information parasitism act**
5 **additively on clutch coverage, whereas interactive effects of these variables were**
6 **assumed in model set 2.**

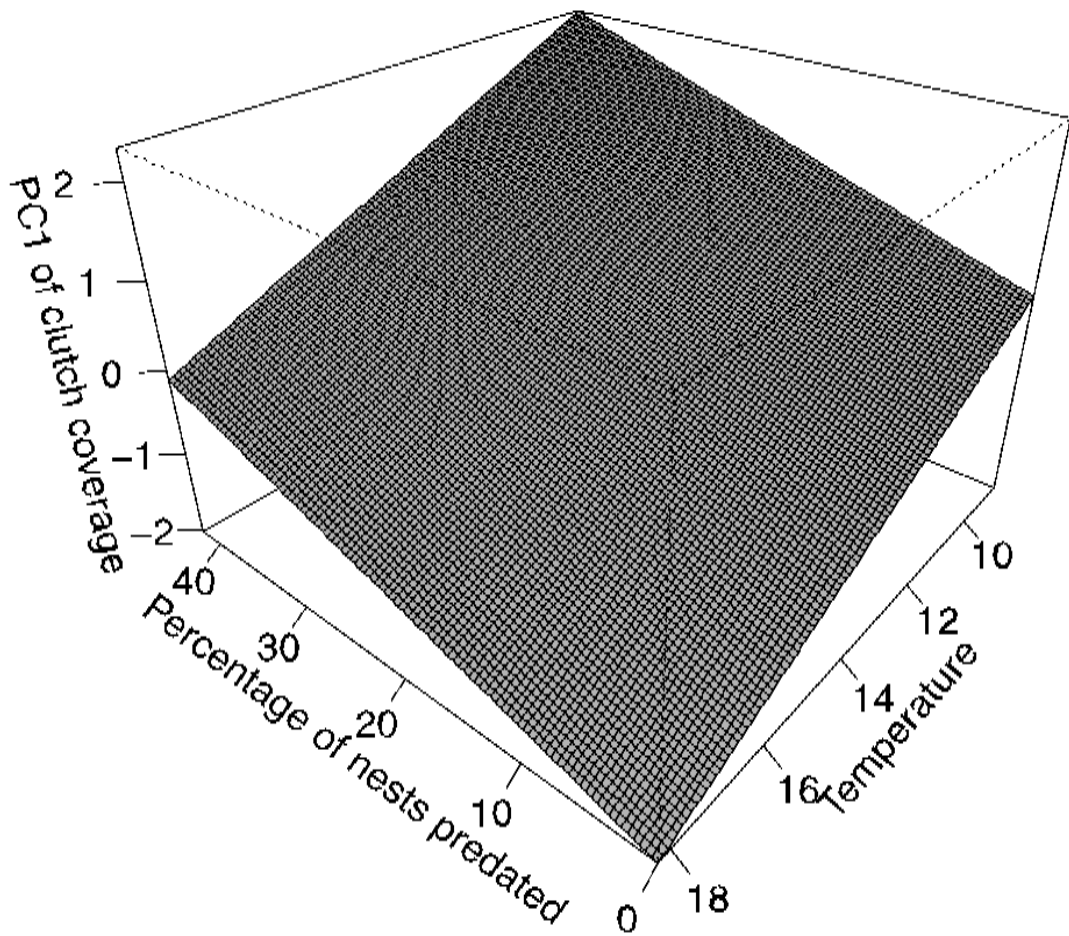
Model set	Variables	Estimate	Adjusted SE	z value	Pr(> z)
a) Model set 1	(Intercept)	1.078	0.556	1.939	0.053
	Nest floor surface	0.009	0.003	3.527	<0.001
	Predation rate	0.045	0.015	3.075	0.002
	Temperature	-0.238	0.046	5.145	<0.001
	*DTG (Citrus)	1.750	0.608	2.876	0.004
	DTG (Fagus)	-0.754	0.679	1.110	0.267
	DTG (Mixed)	0.037	0.541	0.069	0.945
	DTG (Picea)	-0.490	0.427	1.149	0.251
	DTG (Pinus)	0.044	0.418	0.105	0.917
	DTG (Quercus)	-0.453	0.486	0.933	0.351
	Flycatcher density	0.007	0.010	0.686	0.492
	*Geographical location	0.093	0.184	0.505	0.614
b) Model set 2	(Intercept)	1.214	0.643	1.888	0.059
	Nest floor surface	0.010	0.003	2.991	0.003
	Predation rate	-0.013	0.079	0.163	0.870
	Temperature	-0.276	0.085	3.246	0.001
	*DTG (Citrus)	1.988	0.709	2.805	0.005
	DTG (Fagus)	-0.767	0.666	1.151	0.250
	DTG (Mixed)	0.094	0.568	0.166	0.868
	DTG (Picea)	-0.482	0.427	1.129	0.259
	DTG (Pinus)	0.091	0.427	0.213	0.831
	DTG (Quercus)	-0.429	0.491	0.875	0.382
	Flycatcher density	0.010	0.026	0.406	0.685
	*Geographical location	0.074	0.172	0.429	0.668
	Predation rate: Temperature	0.004	0.006	0.723	0.470
	Flycatcher density: Temperature	0.000	0.002	0.138	0.890
	Flycatcher density: Predation rate	0.000	0.001	0.101	0.920
Flycatcher density: Predation rate:	0.000	0.000	0.029	0.977	

7 *DTG = Dominant tree genus.

8 *Geographical location = First principal component of altitude, latitude and longitude

9

10



1
 2 **Figure 2. Regression surface illustrating the relationship between the mean**
 3 **spring temperature (°C), nest predation rate and clutch coverage (first principal**
 4 **component of proportion of clutch covered and mass of the cover material) in**
 5 **great tits. The surface was drawn by using model-averaged parameter estimates**
 6 **based on the assumption of additive effects of mean spring temperature, nest**
 7 **predation rate and flycatcher density (Table 2a) for nest predation rate and mean**
 8 **spring temperature effects, setting dominant tree genus to *Betula* and nest floor**
 9 **surface area to its mean value. Variables that, according to model averaging, did**
 10 **not explain clutch coverage were ignored.**

11
 12

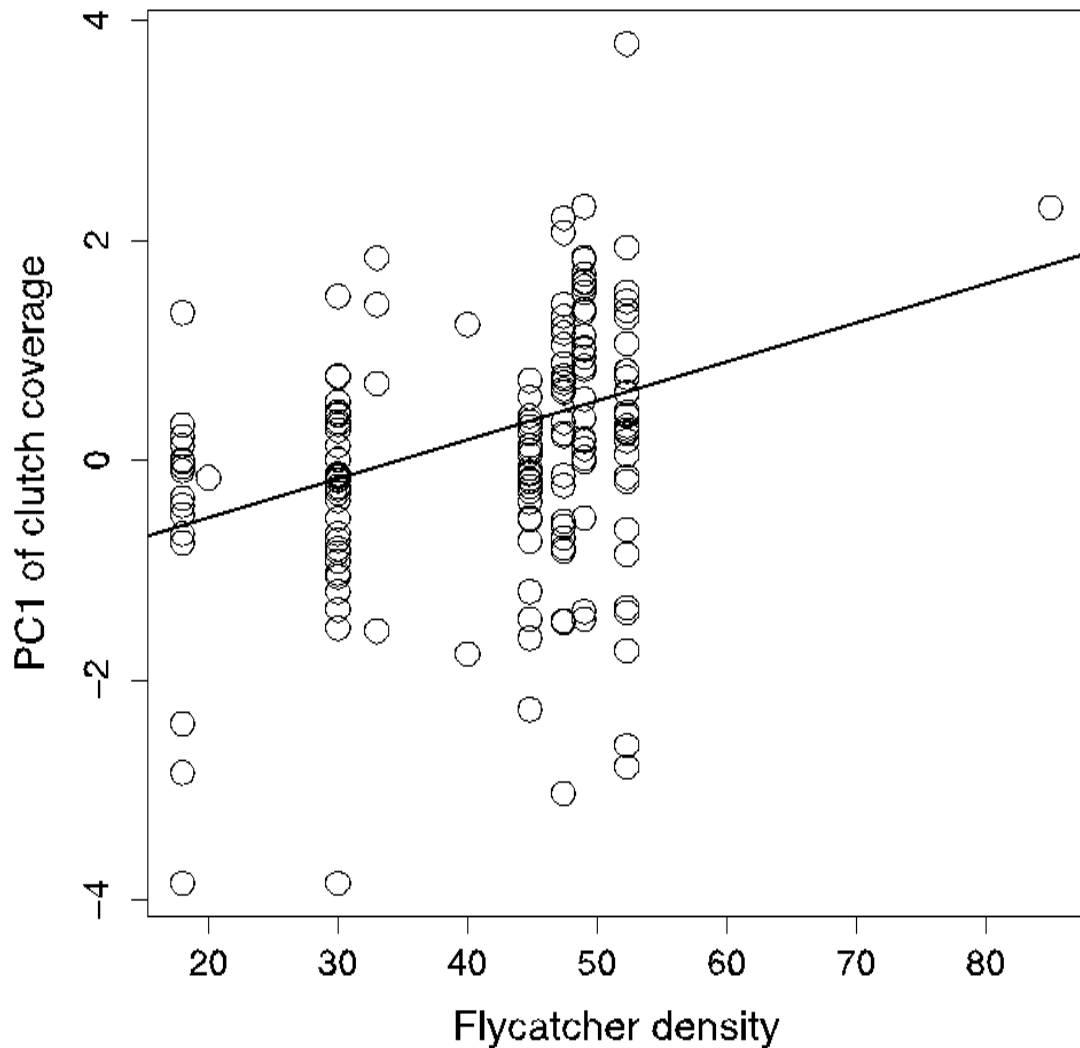
1 **Table 3. Model-averaged (full average) fixed effects of model sets 3 and 4**
 2 **explaining clutch coverage in the great tit in study sites where the flycatchers**
 3 **were present. Model set 3 is based on the assumption that temperature, nest**
 4 **predation and information parasitism act additively on clutch coverage, whereas**
 5 **interactive effects of these variables were assumed in model set 4.**
 6

Model set	Variables	Estimate	Adjusted	z value	Pr(> z)
a) Model set 3	(Intercept)	-1.241	1.182	1.050	0.294
	Flycatcher density	0.036	0.014	2.591	0.010
	Predation rate	0.022	0.014	1.547	0.122
	Temperature	-0.049	0.077	0.634	0.526
	Nest floor surface	0.000	0.002	0.220	0.826
	*DTG (Picea)	-0.001	0.217	0.003	0.997
	DTG (Pinus)	-0.026	0.181	0.142	0.887
	DTG (Quercus)	-0.003	0.279	0.010	0.992
	*Geographical location	0.009	0.111	0.085	0.932
b) Model set 4	(Intercept)	-1.040	1.942	0.536	0.592
	Flycatcher density	0.033	0.033	1.014	0.310
	Predation rate	0.027	0.134	0.204	0.838
	Temperature	-0.065	0.172	0.378	0.706
	Nest floor surface	0.001	0.003	0.257	0.798
	*DTG (Picea)	-0.004	0.219	0.016	0.987
	DTG (Pinus)	-0.032	0.306	0.103	0.918
	DTG (Quercus)	-0.006	0.351	0.018	0.985
	*Geographical location	0.010	0.131	0.074	0.941
	Predation rate: Temperature	0.000	0.004	0.049	0.961
	Flycatcher density: Predation rate	0.000	0.002	0.008	0.994
	Flycatcher density: Temperature	0.000	0.003	0.030	0.976

7 *DTG = Dominant tree genus.

8 *Geographical location = First principal component of altitude, latitude and longitude

9



1

2 **Figure 3. Clutch coverage of great tits in relation to flycatcher density (%) in**
 3 **populations where flycatchers were present. Circles depict data, and the line is a**
 4 **regression line based on model-averaged parameter estimates for flycatcher**
 5 **density effect (Table 3a). Variables that, according to model averaging, did not**
 6 **explain clutch coverage were ignored. The same analysis was repeated without**
 7 **the observation with the highest flycatcher density (>80 %). This did not**
 8 **qualitatively change the model-averaged results (see Supplementary table S17**
 9 **(see Supplementary table S18, for the set of averaged models) and**
 10 **Supplementary figure S4).**

11

12 **4. Discussion**

13 The aim of this study was to investigate large-scale geographical variation in great and
 14 blue tits' egg covering behaviour in Europe and variables that may explain egg covering

1 behaviour. In particular, we test three hypotheses, *the insulation, nest predation and*
2 *information parasitism hypotheses*, suggested to explain the egg covering behaviour of
3 tits. Our results from 28 different populations across Europe show that the clutch
4 coverage of great tits is more extensive with lower mean spring temperature and higher
5 nest predation rate. The analysis also suggest that the increasing flycatcher density is
6 associated with increased egg covering in great tits. However, this effect was found only
7 in populations where breeding flycatchers were present. Despite flycatchers being
8 absent from some study sites, they were breeding in the vicinity of most of these sites,
9 which means that we may have only tit populations with coevolutionary history with
10 flycatchers in our data. The hypothesized mechanisms appear to have additive effects on
11 egg covering behaviour. Thus, these results support the mutually non-exclusive
12 hypotheses that have been put forward to explain egg-covering behaviour in great tits,
13 suggesting that egg covering may have multiple functions. In blue tits, clutch coverage
14 was not associated with any of ecological or abiotic factors, but one should be careful in
15 interpreting these results due to the limited sample size.

16 First, clutch coverage may provide thermal insulation against low temperatures in spring
17 during egg-laying, in a period when the females are not staying in the nest for long
18 periods at a time during the day. This is in line with Haftorn & Slagsvold (1995), who
19 found that egg covering tended to be negatively related to the increasing ambient air
20 temperature in great tits. Also, Loukola *et al.* (2014) found that, in Finland, great tits
21 had 54.5% (0.5 g) more hair on the eggs in Oulu than in Turku. Oulu (latitude 65°) is
22 located over 600 km north of Turku (latitude 60°) and the mean daily spring
23 temperature was 2.4°C cooler (in years 1981–2010) in Oulu (Pirinen *et al.*, 2012).

1 Second, egg covering behaviour might be a protection against nest predators. Yet, it
2 seems unlikely that hair or feather cover could prevent small predators such as weasel
3 (*Mustela nivalis*) or stoat (*M. erminea*) from finding the eggs underneath the covering
4 material. Tits also cover eggs in the populations where mustelids are absent, for
5 example on Gotland, Sweden. However, it is possible that covering the eggs may cheat
6 naive predators into believing that there are no eggs in the nest (Perrins, 1979). Also,
7 predators such as woodpeckers (Picidae), that have small olfactory bulbs (Bang &
8 Cobb, 1968), and thus use mostly visual cues when searching for food, could perceive a
9 nest with covered eggs as an empty nest. If egg covering prevents even some of the nest
10 predation attempts by any of the predators, selection for egg-covering could be
11 expected. This is because the nest predation is among the most important factors
12 affecting the behaviour and life-history traits in birds (Martin & Briskie, 2009). How
13 egg covering affects the behaviour of different predators, remains to be tested.

14 Third, egg covering could be a defence (counter-adaption) to reduce information
15 parasitism. Hiding the clutch size from flycatchers and other competitors makes sense
16 because the clutch size may provide accurate and reliable inadvertent information about
17 the environment and the quality of the tit parents to prospecting birds. Environmental
18 variation explains a large amount of variance in clutch size (Beldal et al., 1998;
19 Charmantier et al., 2006; McCleery et al., 2004; Tremblay et al., 2003) suggesting that
20 clutch size reliably reflects the quality of the environment and can be readily used as a
21 cue about territory quality. Moreover, the clutch size of tits may reveal their competence
22 in cognition and decision making (Cauchard et al., 2017; Cole et al., 2012) and the pied
23 flycatchers have been shown to use clutch size of tits as a primary cue of whether to
24 copy or reject observed tit choices, such as a novel nest site feature preference (Loukola

1 et al., 2013). By covering the eggs, tits would hide this information from flycatchers.
2 Without the information about the tits' success, flycatchers may reject the behaviour of
3 the observed tits more frequently and may be less likely to settle in the immediate
4 neighbourhood of a tit nest. Flycatchers breeding close to tits have a negative effect on
5 tit offspring number and condition (Forsman et al., 2007). Consistent with this, a recent
6 study (Loukola et al., 2013) suggested that flycatchers tended to reject the choices of
7 ostensibly successful tits when the clutch was covered. This, in turn, may reduce the
8 costs of interspecific competition (Loukola et al., 2013).

9 Interspecific exploitation, or eavesdropping (Kroodsma & Miller, 1996), of inadvertent
10 signals is important because it may affect the evolution of extended phenotypes. Usually
11 the evolution of bodily and non-bodily signals are assumed to result from conflicting
12 selection pressures from natural and sexual selection (Schaedelin & Taborsky, 2009).
13 For example, sexual selection may enhance the size and showiness of the nest
14 (Mainwaring et al., 2014; Schaedelin & Taborsky, 2009) while natural selection is
15 expected to reduce the size and the visibility of the nest due to nest predation (Biancucci
16 & Martin, 2010). If information use by other species affects negatively or positively the
17 performance of the species whose extended phenotype is used as a source of
18 information, it brings about coevolution as a potential mechanism affecting the
19 evolution of extended phenotypes. In concert with other recent studies (e.g., Gotelli,
20 Graves, & Rahbek, 2010; Mönkkönen, Devictor, Forsman, Lehikoinen, & Elo, 2017),
21 our results imply that local species interactions can reflect to biogeographic patterns and
22 should also be considered jointly with abiotic factors, which often are solely used to
23 explain large scale patterns.

1 Our results also showed that extent of egg covering increased with increasing nest floor
2 surface area. This suggest that the eggs are spread out over a wider area in nest boxes
3 with larger floor area and more material would be then needed to cover the eggs. Clutch
4 coverage was also affected by the dominant tree genus, being particularly high at site
5 (Sagunto, east Spain) dominated by genus *Citrus*, where several nest
6 competitors/predators (black rats (*Rattus rattus*), house sparrows (*Passer domesticus*)
7 and garden dormouse (*Elomys quercinus*)) occur in high numbers (Barba &
8 Gil- Delgado, 1990; Gil-Delgado et al., 2009). However, leaving the data from Sagunto
9 out from the model set 1 did not change the model-averaged results (Supplementary
10 table S19 (see Supplementary table S20, for the set of averaged models)). One
11 explanation for the differences in clutch coverage among study sites may have been
12 variation in the availability of suitable covering materials. The density and the species
13 composition of local bird and mammal communities, which are linked to various
14 characteristics of the habitat, including tree species, affect the availability of feathers
15 and hairs. The fact that not all tits cover their eggs suggests that some costs are
16 involved. These may include not only the costs of locating and bringing the materials to
17 the nest but the risk of adult predation when collecting. Egg covering materials
18 (mammal hair, feathers) are usually found on the ground where the risk of predation on
19 the female (only the female builds) may be high at a stage where her body mass is high
20 due to the production of eggs. Also, infestation risk by ticks (Ixodidae) is almost
21 entirely limited to lower levels of the vegetation (Humair et al., 1993).

22 The reproductive success of great tits was not significantly associated with clutch
23 coverage. This suggests that egg covering had limited fitness consequences for the tits
24 in the year of study. Year 2013 was phenologically an extremely late year for nesting of

1 forest passerines in most parts of Europe (Gładalski et al., 2016; Wesołowski, Cholewa,
2 Hebda, Maziarz, & Rowiński, 2016, Adriaensen, unpublished data) and it may have
3 affected the reproductive investment decisions of tits in general. Long-term data and
4 manipulative experiments, such as adding/removing covering of eggs or manipulation
5 of temperature within nests (see e.g. Bleu, Agostini, & Biard, 2017) or nest predation
6 risk perception (see e.g. Doligez & Clobert, 2003) could be the next step to test whether
7 the egg covering behaviour is an adaptive trait.

8 **5. Conclusion**

9 Egg covering most likely serves multiple functions in great tits. It provides thermal
10 insulation against cold temperatures and hides the eggs from the nest predators looking
11 for an egg meal and from information parasites searching for clutch-size information.
12 The interactions between the nest predators, information parasites and tits are expected
13 to result in a series of adaptations and counter-adaptations, egg-covering having a
14 function in hiding the eggs. Hence, our results suggest that interspecific interactions also
15 shape extended nest phenotypes of birds, resulting in geographical variation in nest
16 characteristics, depending on the co-occurrence of interacting species. Social
17 information use as a mechanism shaping the extended phenotypes in general has gone
18 unnoticed (Schaedelin & Taborsky, 2009) but is likely to be common in nature. Many
19 extended phenotypes are long-lasting and readily available for coexisting animals that
20 can use them as indicators of food resources or as a source of social information in own
21 decision-making. If other species' utilisation of extended phenotypes has negative
22 consequences for the species whose extended phenotype is utilised, the information
23 content of the extended phenotype is expected to evolve in a direction that reduces such
24 costs. Changing the information content of the extended phenotype, such as egg-

1 covering, is costly in terms of time and energy and there is a lot of variation in this
2 behaviour, both within and between populations. The pattern of geographic variation in
3 tits' egg-covering behaviour is in line with the geographic mosaic of coevolution theory
4 that predicts that interspecific interactions occur at the population scale and may result
5 in different outcomes in different localities (Thompson, 2005). Therefore, geographic
6 variation in species co-occurrences should be taken into account when studying how
7 interspecific interactions affect (co)evolution.

8 **Acknowledgements**

9 OJL was funded by Biological Interactions Graduation School (BIOINT), the Jenny and
10 Antti Wihuri Foundation / the Foundation's Post Doc Pool and Academy of Finland
11 grant no. 24302601. JCS was funded by CGL-2016-79568-C3-3-P research project
12 from the Spanish Research Council (Ministry of Economics and Competitiveness).
13 SMK was funded by Academy of Finland (grants No. 314833 and 319898). JTF was
14 funded by Academy of Finland (grant no. No. 122665 and 125720) and Kone
15 Foundation. The authors declare that there is no conflict of interest.

16 **Authors' contributions**

17 The experiment was designed by OJL and JTF. Data was collected by OJL, PA, FA,
18 EB, BD, EFJ, TE, TL, CM, RM, VR, JMS, MS, JCS, BT, JT and JTF and analysed by
19 OJL, SMK and PTN, and all authors contributed to writing of the manuscript. All
20 authors have read and approved the final manuscript.

21

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25 BIOSKETCH

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