

# Myrmecophily is not a risk factor for long-term occupancy trends of central European Lycaenidae butterflies

## Myrmekophilie ist kein risikofaktor für langfristige vorkommenstrends mitteleuropäischer Lycaenidae

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### Abstract

1. As anthropogenic pressures continue to increase, generalist species tend to be more resilient than specialised species. Specialisation can take various forms, among else dependence on other species through biotic interactions. Some Lycaenid butterflies (gossamer-winged butterflies: blues, coppers and hairstreaks; Lycaenidae Leach, 1815) rely on host ants for larval care and survival (myrmecophily). This dependence may pose an additional threat.
2. To investigate whether myrmecophily is associated with the long-term trends of Lycaenids, we compared 40-year occupancy trends derived from occupancy-detection models of ant-independent, facultative and obligate myrmecophile Lycaenidae in a central European model region.
3. Contrary to our expectations, obligate myrmecophile butterflies did not show more declines compared to ant-independent ones. Five out of seven obligate myrmecophile butterflies increased, while five out of eight ant-independent Lycaenids decreased. Trends among facultative butterflies were highly ambiguous. The differences between the groups were not significant.
4. Although obligate myrmecophile butterflies are protected significantly more often under stricter rules, the degree of protection did not affect Lycaenid long-term trends.
5. European obligate myrmecophile butterflies interact with several ant species within widespread genera (primarily *Myrmica* Latreille, 1804, also *Formica* Linnaeus, 1758

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and *Lasius* Fabricius, 1804) potentially protecting the larvae against environmental impacts and thus mitigating the effects of changing conditions on the butterflies. Incomplete understanding of the varying degrees of ant affiliation hinders the identification of specific interactions that may require increased conservation efforts.

6. In our rapidly changing world, monitoring changes in the opportunities and strengths of species interactions is needed to prevent coupled species' extinctions and improve conservation outcomes.

#### KEYWORDS

ant, biodiversity monitoring, butterfly, Germany, insect conservation, long-term trend, occupancy-detection model, specialisation

## INTRODUCTION

Insect declines, be it in abundance, diversity or distribution, have become apparent in recent years (e.g., Hallmann et al., 2021; Wagner et al., 2021). Due to their importance for human well-being as providers of highly valuable ecosystem services (Leonhardt et al., 2013; Ollerton et al., 2011; Winfree et al., 2007), pollinator declines especially have become increasingly recognised by the public. In an effort to conserve biodiversity, certain butterflies have been designated as 'flagship' species, such as the large blues (*Phengaris* Doherty, 1891–Lycaenidae Leach, 1815; Thomas & Settele, 2004). These species play an important role in communicating about insect conservation (Oberhauser & Guiney, 2009). Lycaenid butterflies are also among butterfly families with severe long-term declines (Habel et al., 2019).

Insect trends are not equal among species, and identifying the drivers of species trends is crucial for successful conservation efforts. In general, specialist species are decreasing while generalists show increasing trends. Various forms of specialisation, such as habitat or food source dependence, have been shown to contribute to species declines (Biesmeijer et al., 2006; Dantas de Miranda et al., 2019; Roth et al., 2021), especially in butterflies (Engelhardt, Biber, et al., 2022). Therefore, considering different types of specialisation is an important aspect when assessing species' trends (Eskildsen et al., 2015; Schleuning et al., 2020).

Specialisation can also arise in distinct interactions with other species, which can govern species' occurrences at least as much as abiotic conditions (García-Girón et al., 2020; Wisz et al., 2013). A fascinating example for biotic interactions is myrmecophily, which generally describes a biotic interaction with ants during part of a species' lifecycle (Hölldobler & Wilson, 1990; Kronauer & Pierce, 2011). Myrmecophily independently evolved in a variety of taxonomic groups, for example, in insects from beetles and butterflies to crickets, flies and wasps. In Lycaenid butterflies, myrmecophily developed independently numerous times and also lead to rapid radiations (Pierce et al., 2002).

A majority of Lycaenid butterflies have facultative or obligate interactions with ants that range from mutualism to parasitism (Fiedler, 1991, 2006; Pierce et al., 2002). So-called ant guests—the caterpillars—live inside ant nests. The ant colonies provide a stable food source as well as protection, both from predators and abiotic

influences, creating a stable microclimate that can persist for several decades. Some Lycaenids have a mutualistic symbiosis with their ant hosts, in which the caterpillars secrete a honeydew-like substance, which contribute to the nutrition of the ants, while the ants protect the caterpillars in their burrows (Fiedler & Maschwitz, 1988). Others, like the genus *Phengaris*, are social parasites specialised on ants of the genus *Myrmica* Latreille, 1804, in which the caterpillars either mimic ant larvae to be fed by the ants or feed on the ant brood. Therefore, especially the latter reduces host ant fitness (Tartally et al., 2019) and where ants detect parasitic caterpillars, they become a threat for the butterflies. While obligate myrmecophile butterflies are specialised at least to the genus-level of their ant partners, facultative associations are opportunistic and unpredictable (Fiedler, 2021), although more common than obligate associations.

Here, we hypothesize that dependence on ant species might pose a threat for butterflies (Pierce et al., 2002). We compare 40-year occupancy trends of Lycaenid butterflies not interacting with ants to those of facultative and obligate myrmecophile Lycaenids, in a central European region. We expect obligate myrmecophile Lycaenids to present more decreasing trends than ant-independent Lycaenids, based on the pervasive negative effects of specialisation on trends.

## METHODS

### Butterfly annual occupancy estimates

We based our analysis on 40-year annual occupancy estimates (Engelhardt, Biber, et al., 2022) for 37 Lycaenidae butterflies across the federal state of Bavaria, Germany (Figure S1, 70,542 km<sup>2</sup>). We derived occupancy estimates from occurrence records of 176 butterfly species (Lepidoptera, Rhopalocera) reported between 1980 and 2019, collected by the Bavarian Environment Agency (Bayerisches Landesamt für Umwelt/LfU), and both the species records and occupancy models were validated by experts. Occupancy-detection models are hierarchical models combining a state sub-model estimating each species' occupancy per location and year with an observation sub-model describing the detection probability for each species on a given visit to each location and year. For details on the modelling process, see Engelhardt et al. (2022). The dataset provides mean occupancy

estimates, associated uncertainties (standard deviation and 95% CI), and model evaluation scores for each year and species (compare Figure S2). We evaluated annual occupancy estimates based on the Gelman–Rubin statistic (Rhat, Gelman & Rubin, 1992), a measure of model convergence where Rhat values above or equal 1.1 indicate non-convergence. We calculated the mean Rhat values of the annual occupancy estimates of the 44 Lycaenidae present in Bavaria and excluded butterflies whose mean Rhats were above or equal 1.1. In addition, we excluded species with occupancies of less than 0.025 across all study years, that is, very rare species. Additionally, we treated the cryptic species *Aricia [Polyommatus] agestis* ([Denis and Schiffermüller], 1775) and *A. artaxerxes* (Fabricius, 1793) as one species in the dataset and corresponding modelling process; thus, we excluded those as well (compare Table S1).

### Attribute data

We used a dataset that compiles data on global Lycaenidae–ant interactions by Fiedler (2021), which includes all Lycaenids from our study region. We compared the information of this dataset to other sources (Fiedler, 1991; Kühne et al., 2001; Middleton-Welling et al., 2020; Tartally et al., 2019) to ensure reliable classifications. Of the 37 Lycaenids analysed (Table S2), seven are obligate myrmecophile, eight are ant-independent and 22 butterflies are facultative myrmecophile with differing degrees of strength in the ant–butterfly connection (Fiedler, 1991). The exact number of ant species and genera interacting with each butterfly is limited by current knowledge, especially for facultative butterflies. Most datasets on Lycaenid myrmecophily treat the two types of populations of *Phengaris alcon* ([Dennis and Schiffermüller], 1775), *Ph. alcon H* and *Ph. alcon X*, as one species only Fiedler (2021) reports differing obligate ant associations of the two ecotypes (based on Tartally et al., 2008, 2019, 2014). Thus, we treated both ecotypes separately as obligate myrmecophile. We also obtained information on the conservation status of ants interacting with obligate myrmecophile butterflies based on the most recent red lists for the study region, although the trends may be dated (Seifert, 2011; Sturm & Distler, 2003), see Table S3.

To account for other possible drivers of butterfly trends, we checked whether the groups differed in terms of their habitat and temperature preferences, based on Engelhardt, Biber, et al. (2022), as well as their protection status (Table S4). If ant-independent, facultative and obligate myrmecophile butterflies differ in these, any difference in their trends could be explained by the impacts of climate change, land use change or conservation measures. For temperature preference, we used each butterfly's median annual temperature in their European range (cf. Devictor et al., 2012), based on Atlas data from Kudrna et al. (2011) (spatial extent 10° W, 30° E, 35° N and 71° N) and Euro-Cordex climate data compiled using the R-package DISMO (Hijmans et al., 2020). For habitat preference, we obtained information on the Lycaenid's main habitat as well as the number of different habitat types each butterfly inhabits from the Bavarian atlas of butterfly species (Bräu et al., 2013) and a German butterfly

identification guide (Settele et al., 2005). We collated butterfly protection programmes from the Bavarian environment agency (Bayerisches Landesamt für Umwelt, 2024), the German Federal Nature Conservation Act (Bundesministerium für Umwelt Naturschutz und nukleare Sicherheit (BMU), 2005) and the European Habitats Directive (European Commission, 2021).

### Linear trends

We calculated each butterfly's 40-year linear trends as well as the mean trends of all Lycaenids. We fitted Bayesian generalised linear models with annual occupancy estimates from 1980 to 2019 as the response and year as the only predictor. We used the BRM function from the R-package BRMS (Bürkner, 2017) via STAN (Stan Development Team, 2022b) and RSTAN (Stan Development Team, 2022a). We included the standard deviation of the annual occupancy estimates as a source of measurement error (using the *mi* function) to account for the uncertainty of the mean occupancy estimate in all models. Each butterfly model as well as models across all ant-independent, facultative and obligate myrmecophile Lycaenids were run separately. We ran all models with three sets of priors for fixed effects: narrower normal (0,1) priors, slightly narrower normal (0,10) priors and default, flat priors. We used four chains with 4000 iterations and a warmup of 2000 each. The step of the algorithm was 0.99999 and we used a tree depth of 12. All models show good convergence (Rhat <1.1), and we report results of models with lowest Rhats. The different priors led to similar results. We report linear trends where the 95% credible intervals (CIs) are larger than zero as increasing, where the 95% CIs are smaller than zero as decreasing and where the 95% CIs overlap zero as stable.

### Attribute analysis

To analyse differences in trends among ant-independent, facultative or obligate myrmecophile Lycaenid butterflies, we applied Bayesian generalised linear mixed-effects models using the R-package BRMS (Bürkner, 2017). The response variable was each butterfly's annual occupancy estimate, with model uncertainty captured by each estimate's standard deviation (using the *mi* function). We used models with a beta distribution, as the occupancy estimates were bounded between zero and one. Explanatory variables were year, as a continuous variable, and ant association as a factor (facultative vs. obligate myrmecophile vs. ant-independent), along with their interaction. We included the butterflies as a random effect, allowing for random intercepts and random slopes for year. We ran our models with 4000 iterations and four chains, warmup of 2000, tree depth of 12, algorithm step of 0.999999 and set the initial value to 0.1. We used three sets of priors for the fixed effects (narrower normal(0,1), slightly narrower normal(0,10), and the default, flat priors). For the other parameters, we used the default priors. We reported models with a normal (0,10) prior for fixed effects, yielding similar results with alternative priors.

We applied Bayesian generalised linear models to test whether other potential drivers could explain differences in trends of ant-independent, facultative and obligate myrmecophile Lycaenids. We assessed whether the groups differed in their degree of habitat specialisation, their temperature preference and protection status by using myrmecophily as explanatory variable and the number of habitats, temperature preference (scaled and centred) or number of protection schemes as the response, respectively. We ran 2000 iterations and four chains with a warmup of 1000.

We applied Bayesian generalised linear mixed-effects models again to assess whether the protection status with and without interaction with myrmecophily influenced Lycaenids' long-term trends. Here, the explanatory variables were year, as a continuous variable and protection status, as a continuous variable (0—no protection scheme, 1—German Federal Nature Conservation Act, 2—Lycaenid-specific programme and/or Habitats Directive in addition to the German Federal Nature Conservation Act—same results obtained treating protection as a binary variable), as well as their interaction. To check whether the protection status in combination with the ant-dependence influenced butterfly long-term trends, the explanatory variables were year, ant interaction and protection status as well as their interactions. Here, we increased the number of iterations to 6000 and used a narrower normal (0,1) prior for fixed effects to receive reliable model results.

All models showed high convergence with Rhats <1.1 for all coefficients. The analyses were conducted using R version 4.2.0 (R Core Team, 2022). For further details, refer to Data S1: Supporting Information: Code.

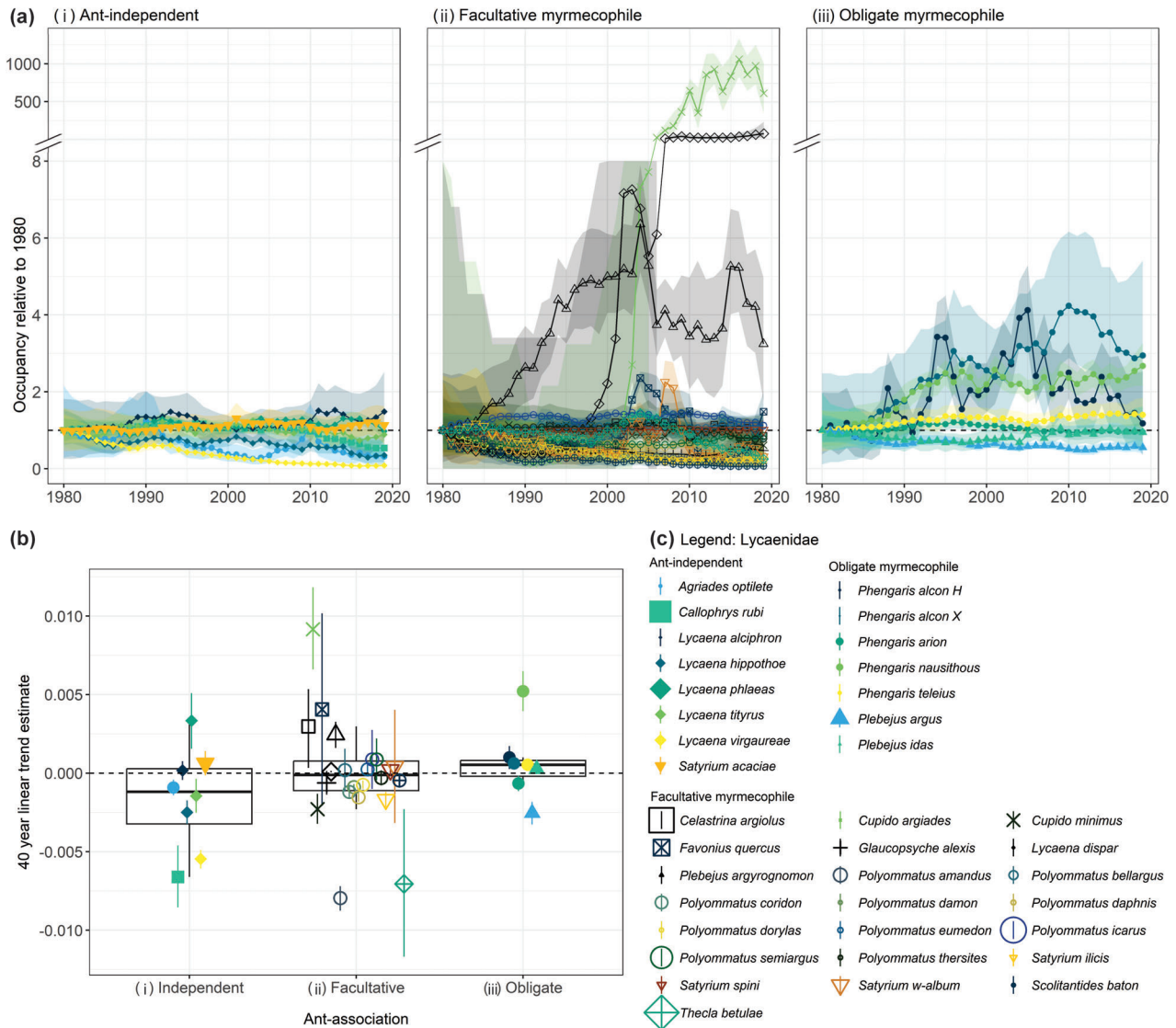
## RESULTS AND DISCUSSION

Contrary to our expectation, 40-year trends of Lycaenid butterflies with an obligate interaction with ants did not differ from those of ant-independent or facultative Lycaenids. Across all Lycaenidae, 16 (43%) butterflies decreased, 10 (27%) increased and 11 (30%) showed stable or unclear trends. The long-term trends of obligate myrmecophile Lycaenids were more positive, on average, than those of facultative myrmecophile or ant-independent butterflies (mean trend: obligate myrmecophiles = 0.0007, 95% CI = -0.0004 to 0.0018; facultative myrmecophiles = -0.0001, 95% CI = -0.0014 to 0.0012; ant-independent Lycaenids = -0.0015 to 95% CI = -0.0035 to 0.0004; Figure 1b (ii)), but the 95% CI of their trend differences overlapped zero (95% CIs: ant-independent compared to obligate myrmecophile = -0.0516 to 0.0766; ant-independent compared with facultative myrmecophile = -0.0238 to 0.0687). Of the obligate myrmecophile Lycaenids, there were five increasing butterflies and two decreasing (Figure 1a (iii), Table S2). Nine facultative myrmecophile Lycaenids decreased and four increased (Figure 1a (ii)). Meanwhile, five out of eight ant-independent Lycaenids decreased, and only one butterfly increased significantly (Figure 1a (i)). Thus, although a large proportion of Lycaenids in our study area have decreased, obligate myrmecophily was not a risk factor for occupancy changes.

Myrmecophile butterflies prefer ant species that persist for multiple years (Fiedler, 2021; Hölldobler & Wilson, 1990). This preference might increase their resilience to environmental change such as the direct effects of climate warming; however, phenological mismatches of interacting species (e.g. Visser et al., 2012) could become more likely as the climatic stability of the ant colony and thus of the butterfly's phenology could stand in contrast to changes in host plant phenology, which would especially increase the risks for monophagous butterflies. In addition, delayed responses to threats by ant colonies could result in a lag in the decline of butterfly populations, making it harder to identify the source of the decline. Another factor of uncertainty is intraspecific variability in the interaction between caterpillars and ants. For instance, in some *Ph. alcon* X populations, a quarter of the caterpillars parasitize ant hosts for only half the time of the remaining caterpillars, yet the pupae of both groups attain the same size (Thomas et al., 1998). Such variability might allow the butterflies to adapt to changing conditions.

Sheard et al. (2021) suggest that butterflies depending on declining ant species might show coupled declines. Of the 87 ant species present in the study region, 59 (68%) are listed in the Bavarian Red List of endangered species in one of the threat categories (extinct, critically endangered, endangered, vulnerable or data deficient but assumed to be endangered). Another eight species (9%) are near threatened and declining (Sturm & Distler, 2003), see Table S3. A possible candidate for a coupled decline could be *Phengaris arion* (Linnaeus, 1758), which across the European continent relies on nine *Myrmica* ant species also present in Germany, where one is classified as endangered, three as vulnerable and another three as near threatened and declining in the study region (Seifert, 2011). In Germany, only interactions with one ant species classified as near threatened and declining, *Myrmica sabuleti* (Meinert, 1861), has been proven so far, and the species tends to specialise on one locally most common *Myrmica*-host (Tartally et al., 2019). The second declining obligate myrmecophile butterfly, *Plebejus argus* (Linnaeus, 1758), is the only Lycaenid that relies solely on ant species of the genus *Lasius* Fabricius, 1804. One species of this genus, *Lasius alienus* (Förster, 1850), is considered endangered on the regional red list (Sturm & Distler, 2003; see Seifert & Galkowski, 2016 on the *L. paralienus* group), whereas the other two species known as butterfly associates are not listed. An effect of the ant genus cannot be determined, as the other obligate myrmecophile Lycaenids interact with ants of the genus *Myrmica* or *Formica* Linnaeus, 1758. Our understanding of these interactions is limited, and even less is known about facultative myrmecophile Lycaenids. In addition, there has not been an assessment of changes in ant distribution in our study region thus far, and species records are limited (Sturm & Distler, 2003). These knowledge gaps underscore the need for further research to better understand the ecological dynamics of these interacting species.

The availability of ant hosts might affect butterfly local abundances more than their regional distribution. Abundances and distribution changes can be uncoupled (Dennis et al., 2019), and when correlated, distribution trends likely underestimate changes in species abundance (Buckley & Freckleton, 2010; Webb et al., 2012).



**FIGURE 1** Comparison between 40-year occupancy trends of ant-independent and obligate myrmecophile Lycaenid butterflies. (a) Annual occupancy estimates relative to each butterfly's occupancy estimate of 1980 of (i) ant-independent, (ii) facultative and (iii) obligate myrmecophile Lycaenidae from 1980 to 2019. Ribbons indicate relative 95% credible intervals of the occupancy estimates. (b) Boxplots of ant-independent and obligate myrmecophile butterflies' linear trends (1980–2019). Point ranges indicate single butterfly trends with error bars representing the 95% credible intervals. Shapes detailed in (c) indicate the genus (Ant-independent: points—*Agrionides* Hübner, 1819; squares—*Callophrys* Billberg, 1820; rhombus—*Lycaena* Fabricius, 1807; triangles—*Satyrion* Scudder, 1876; Obligate myrmecophile: triangles—*Plebejus* Kluk, 1780; points—*Phengaris*; Facultative myrmecophile: squares—*Celastrina* Tutt, 1906, X—*Cupido* Schrank, 1801; square with X—*Favonius* Sibatani and Ito, 1942; plus—*Glaucopteryx* Scudder, 1872; rhombus—*Lycaena*, triangle—*Plebejus*; circle—*Polyommatus* Latreille, 1804; top-down triangle—*Satyrion* Scudder, 1876; circle with plus—*Scolitantides* Hübner, 1819; rhombus with plus—*Thecla* Fabricius, 1807) and the colour defines the butterfly. The size of the symbols in the legend indicates each Lycaenid's occupancy in 1980, compare Table S2 for precise values. See Figure S5 for single butterfly occupancy models.

This could be the case for the two obligate myrmecophile Lycaenids declining in our study, *Phengaris arion* and *Plebejus argus*. *Ph. arion* is listed as endangered on the regional butterfly red list (Voith et al., 2016) with strong population declines but shows only slight, though significant declines in occupancy (annual trend estimate  $-0.0007$ , 95% CI =  $-0.0011$  to  $-0.0002$ ). *Plebejus argus*, however, is only listed as near threatened on the red list but shows significant occupancy declines (annual trend estimate  $-0.0025$ , 95%

CI =  $-0.0033$  to  $-0.0018$ ). This discrepancy highlights the need for multi-scale analyses to assess different metrics of species change.

Neither temperature preference nor habitat specialisation differed between the groups (95% CIs of difference, temperature preference: ant-independent compared to obligate myrmecophile =  $-0.84$  to  $1.22$ , ant-independent compared to facultative myrmecophile =  $-0.02$  to  $1.61$ , Figure S3A; number of habitats: ant-independent compared with obligate myrmecophile =  $-2.16$  to  $0.77$ , ant-independent compared to

facultative myrmecophile =  $-0.88$  to  $1.43$ , Figure S3B). Therefore, when comparing ant-independent to obligate myrmecophile Lycaenid butterflies, differences in temperature preference and habitat breadth do not affect our results. Most Lycaenids are habitat specialists of grasslands. One ant-independent and four facultative myrmecophile Lycaenids are habitat generalists. Across Europe, grassland specialist butterflies have typically declined (Van Swaay et al., 2019).

Of the Lycaenids analysed 26 are protected in the study region. The degree of protection is significantly higher for obligate myrmecophile butterflies compared with ant-independent Lycaenids (95% CI of difference: 0.32, 1.57) with five species protected under the Habitats Directive in addition to the German Federal Nature Conservation Act, but that did not affect butterfly trends (95% CI of protection effect on occupancy over time:  $-0.036$ ,  $0.033$ ; for obligate myrmecophile compared with ant-independent Lycaenids:  $-0.094$ ,  $0.106$ ; compare Data S1: Supporting Information: Code). For two Lycaenids, additional conservation programs are in place in the study region. *Phengaris alcon* X has been successfully protected since 2003 and showed an increasing trend (Figure 1a (iii); Table S2). In recent years, it showed an expansion into the surroundings of the city of Munich about 40–50 km away from known populations (Morawietz et al., 2023). Contrary, the second species, *Polyommatus damon* ([Denis and Schiffermüller], 1775), which is protected under three programs since 2006, nevertheless showed a decreasing distribution trend. Similarly, three of the butterflies listed in the Habitats Directives annexes showed increasing trends (*Lycaena dispar* ([Haworth], 1802), *Ph. nausithous* (Bergsträsser, 1779), *Ph. teleius* (Bergsträsser, 1779)) while another decreased (*Ph. arion*). Of the ant species, four were protected under the German Federal Conservation Act (*Formica exsecta* (Nylander, 1846), *F. lugubris* (Zetterstedt, 1838), *F. pratensis* (Retzius, 1783), *F. pressilabris* (Nylander, 1846)), all interacting with *Plebejus idas* (Linnaeus, 1761), who showed a positive trend. Therefore, there was no consistent effect of the conservation programs on Lycaenids' distribution trends (Engelhardt et al., 2023). Considering the requirements of different host ants when preserving habitats may help ant populations and, in turn, myrmecophilous butterflies.

Even for well-studied insect groups like central European butterflies, detailed knowledge of many aspects of their biology is yet unknown, although it could help understand their long-term trends in the face of environmental change. One such aspect could be migratory behaviour, where we know of some Lycaenids that undergo mass migration events (like *Lycaena hippothoe* (Linnaeus, 1761), *L. phlaea* (Linnaeus, 1761), *Polyommatus coridon* (Poda, 1761), *P. icarus* (Rottemburg, 1775), *P. semiargus* (Rottemburg, 1775)) and others, where parts of their populations show differing migratory or resident behaviour (like *Cupido argiades* (Pallas, 1771), *Celastrina argiolus* (Linnaeus, 1758)) (Chowdhury et al., 2021; Parmesan et al., 1999). All these butterflies displayed ambiguous trends in our study area. However, we cannot draw any conclusions about the effects of such attributes without more knowledge of their life cycles.

Identifying drivers of species' trends is essential for successful conservation action. While dependence on other species is a general risk factor (Biesmeijer et al., 2006; Merckx & Van Dyck, 2019; Roth

et al., 2021; Weiner et al., 2014), the occupancy trends of obligate myrmecophile butterflies do not differ from those of ant-independent or facultative myrmecophile Lycaenidae in our study area, and even show slightly more positive trends. As climate change is rapidly increasing, interacting species might react differently to changing conditions (Schleuning et al., 2020). Careful monitoring is needed to assess how species' populations are developing, and modelling methods like occupancy-detection models can be used to smooth out differences in annual sampling efforts. Additionally, species distribution models could be used to assess possible future occurrences of interacting species. These methods could help identify those interactions possibly under threat in the future and thus in need of close monitoring and specific protection efforts. However, such models are only useful if enough basic knowledge about species interaction partners and their distributions is known, highlighting the need for field observations and expert knowledge which should be integrated with solid modelling approaches. These examples show how different aspects of ecological research could and should be combined for successful conservation action.

## AUTHOR CONTRIBUTIONS

**Eva Katharina Engelhardt:** Conceptualization; methodology; software; data curation; investigation; validation; formal analysis; visualization; writing – original draft; writing – review and editing. **Diana E. Bowler:** Methodology; investigation; validation; supervision; writing – review and editing. **Matthias Dolek:** Validation; writing – review and editing. **Melvin Kenneth Opolka:** Validation; writing – review and editing. **Christian Hof:** Supervision; resources; project administration; funding acquisition; writing – review and editing; investigation.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Butterflies' annual occupancy estimates and code for occupancy models are available under doi:10.5061/dryad.4f4qrjff5. Attribute data is available from Fiedler (1991, 2021), Kühne et al. (2001), Middleton-Welling et al. (2020), Engelhardt, Biber, et al. (2022), as well as from the Bavarian atlas of butterfly species (Bräu et al., 2013)

and the Bavarian Red List for ant species (Sturm & Distler, 2003). Code for analyses uniquely used here is available in Data S1: Supporting Information: Code.

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## SUPPORTING INFORMATION

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

**Data S1.** Supporting Information Code.

**Figure S1.** Overview of the study region Bavaria and the data basis.

(a) Location of the study region in Europe (grey coloured area) and detailed geographic map of the federal state of Bavaria, Germany



(70,542 km<sup>2</sup>), where colouration indicates the geographical relief, lakes and rivers received from the General Bathymetric Chart of the Oceans (GEBCO Compilation Group, 2022), while red areas mark large cities. Borders and cities were received from Eurostat (2022). DXX indicate main natural units, see Bayerisches Landesamt für Umwelt (2021). Courtesy of Jan Kalusche. (b) Number of years with butterfly observations between 1980 and 2019 for each grid cell (appr. 5 × 5 km grid) ranging from zero (white) to 35 years (dark blue) with observations of the 40-year study period. (c) Number of Lycaenids observed between 1980 and 2019 for each grid cell ranging from zero (white) to 29 Lycaenids (dark red) observed within one grid cell of 37 butterflies considered in the study.

**Table S1.** Butterflies excluded from analysis from full Lycaenidae species list. Criterion 1: minimum occupancy (min occ.) of 0.025 in at least one year (min occ.) not reached. Criterion 2: Model quality exceeds the limits of mean  $Rhat \geq 1.1$  and/or mean standard deviation (SD)  $\geq 0.1$ .

**Table S2.** Butterflies included in the analyses: Ant-independent, facultative and obligate myrmecophile and Lycaenidae, their annual linear trend estimates with lower and upper credible intervals (CI). Occupancy in the year 1980, the beginning of our study period. Maximum number of grid cells ( $N$  Grid Cells–Max), where each Lycaenid had been observed in a single year between 1980 and 2020 and the total number of distinct grid cells ( $N$  Grid Cells–Total), where each Lycaenid had been observed during the whole study period.

**Table S3.** Obligate myrmecophile Lycaenids and their associated ant species according to Fiedler (2021) and Tartally (2019) present in the study region. Trend estimate = Lycaenid 40-year linear trend estimates rounded to four digits;  $N$  Ant Gen. = number of associated ant genera;  $N$  Ant = number of associated ant species present in the study region / number of known ant hosts; Ant Species = ant associates of the Lycaenid butterfly; species under special protection under the German Federal Nature Conservation Act (BArtSchV Anlage 1 zu § 1) are underlined.; Red List = the ant species' red list status for Bavaria from the Bavarian Red List (Sturm & Distler, 2003) and for Germany from the German Red List (Seifert, 2011). German Red List categories: 0 = extinct ('Ausgestorben oder verschollen'); 1 = critically endangered ('Vom Aussterben bedroht'); 2 = endangered ('Stark gefährdet'); 3 = vulnerable ('Gefährdet'); V = near threatened and declining ('Vorwarnliste'); G = data deficient but assumed to be endangered ('Gefährdung anzunehmen, aber Status unbekannt'); \* = least concern ('nicht gefährdet'); D = data deficient ('Daten defizitär'); -: not evaluated.

**Figure S2.** Single butterfly occupancy plots, grouped by ant association and plotted in alphabetical order. The annual proportion of

occupied sites in the study area (State of Bavaria, Germany) for each Lycaenid is shown from 1980 to 2019. As estimated with the Gelman–Rubin statistic, the blue circles show satisfactory model convergence ( $Rhat < 1.1$ ) and red points suggest unacceptable model convergence ( $Rhat \geq 1.1$ ). Unfilled circles indicate that a butterfly was not found in the study region in that year. Filled circles indicate a Lycaenid observation in the study area and year. Grey ribbons represent 95% credible intervals.

**Table S4.** Further factors which could affect butterflies' long-term trends. Relationship (Rel.) with ants: ind.—independent, fac.—facultative myrmecophile, obl.—obligate myrmecophile. Temp Pref [degree Celsius]: butterfly temperature preference as median annual temperature across their European distribution in degree Celsius (compare Engelhardt et al., 2022 for details). Habitat Class: Specialists with up to three different habitat types, generalists with at least four different habitat types. Main habitat indicates a rough description of each Lycaenid's preference, habitat type (Hab. Type) is an even broader description. Habitats gives more detailed information on the habitats inhabited. Habitat information based on Bräu et al., 2013; Settele, Steiner, Reinhardt, Feldmann, & Hermann, 2005.

**Figure S3.** Further factors which could affect butterflies' long-term trends, but do not differ between the groups of each ant association. (a) Lycaenidae 40-year trend estimates per main habitat type in the study region; (b) butterfly temperature preference as median annual temperature across their European distribution in degree Celsius for each ant association (ant-independent, facultative or obligate myrmecophile). Shapes indicate the genus (Ant-independent: points—*Agriades* (Hübner, 1819); squares—*Callophrys* (Billberg, 1820); rhombus—*Lycaena* (Fabricius, 1807); triangles—*Satyrium* (Scopoli 1777); Obligate myrmecophile: triangles—*Plebejus* (Kluk 1780); points—*Phengaris*; Facultative myrmecophile: squares—*Celastrina* (Tutt 1906); X—*Cupido* (Schrank 1801); square with X—*Favonius* (Fabricius 1807); plus—*Glaucopsyche* (Scudder 1872); rhombus—*Lycaena*, triangle—*Plebejus*; circle—*Polyommatus* (Latreille 1804); top-down triangle—*Satyrium* (Scudder 1876); circle with plus—*Scolitantides* (Hübner 1819); rhombus with plus—*Thecla* (Fabricius 1807)) and colours specify the butterfly.

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