

Climate and parasite pressure jointly shape traits mediating the coevolution between an ant social parasite and its host

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Handling editor: Alejandro Gonzalez-Voyer, Associate editor: Tim Janicke

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Abstract

Host–parasite relationships are often shaped by coevolutionary arms races. While abiotic influences on these dynamics are well documented, a combined analysis of abiotic and biotic factors is essential for understanding coevolution, particularly under climate change. In this study, we analysed the interactions of the obligate social parasite *Temnothorax americanus*, a dulotic ant, and its primary host, the ant *T. longispinosus*, focusing on behavioural and cuticular hydrocarbon (CHC) traits that govern parasite invasion and host defence. We studied the link between these traits and local climate as well as parasite prevalence. Our results revealed that behavioural interactions were more strongly associated with climate than parasite prevalence. Hosts from warmer, drier regions exhibited reduced aggression during parasite encounters, opting to pick up the brood and flee, while parasites from these regions exhibited greater aggression and activity. CHCs mediating enemy recognition in these ants were linked to local climate and parasite prevalence in both species. As all colonies were maintained under standardized conditions for a year, we attribute the observed phenotypic traits to evolutionary adaptation rather than phenotypic plasticity. Our findings suggest that both abiotic and biotic factors play critical roles in shaping co-evolving traits, sometimes leading to unexpected patterns that would potentially be overlooked when considering only a single factor. These insights provide a framework for understanding how climate influences coevolution of interacting species.

Keywords: coevolutionary arms race, bioclimatic gradient, climate, nestmate recognition, social parasites

Introduction

Climate influences the structure and function of ecosystems, often exerting spatially heterogeneous effects that differentially impact species phenology, geographic distribution, as well as community composition and dynamics (Walther et al., 2002). Species interactions cannot be fully understood without accounting for the environmental conditions in which they occur (Ockendon et al., 2014; Poisot et al., 2017). For example, climate change can facilitate parasite exploitation by altering the host immunometabolism, as warmer temperatures boost parasite growth and reproduction while inhibiting host immune responses (Scharsack et al., 2021). This is particularly evident in ectothermic hosts and parasites, where interaction dynamics depend on the physiological and behavioural adaptations of each partner to key environmental factors such as temperature (Franke et al., 2019; Ragonese et al., 2024). Moreover, these factors may interact in complex ways influencing host–parasite relationships. For instance, while drought and elevated temperatures independently enhance parasitoid effects on aphid populations, their combined effects negatively impact parasitoids (Romo & Tylanakis, 2013). Therefore, assessing the influence of abiotic factors is

essential for understanding the coevolutionary dynamics of host–parasite interactions.

Insects protect themselves from desiccation with a layer of cuticular hydrocarbons (CHCs) covering their cuticle, which represents a crucial adaptation serving multiple functions (Sprenger & Menzel, 2020). Water retention is thought to be primarily achieved by hydrocarbons with high melting points, such as linear alkanes (*n*-alkanes), that typically convey little informational content (Bonavita-Cougourdan et al., 1987). However, CHCs also play a key role in communication, particularly in social insects, mediating nestmate recognition and influencing behavioural interactions. Nestmate recognition relies on structurally more complex molecules, including methylated alkanes and alkenes, which encode information on individual and colony identity. As these substances melt at lower temperatures, they are less effective at preventing water loss (Gibbs, 1995; Menzel et al., 2019). At the colony level, a relatively uniform colony odour is generated through the mixing of individual chemical profiles via mutual grooming (Lenoir et al., 2001b). This chemical signature is learned early in life, stored, and updated as a neural template in the ant's brain, enabling individuals to distinguish outsiders with qualitatively and/or quantitatively distinct CHC profiles (Blomquist

Received March 13, 2025; revised July 30, 2025; accepted August 2, 2025

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& Bagnères, 2010). When two ants meet, they compare each other's CHC profiles to assess whether the other one is a nestmate. The likelihood of aggression (i.e., recognition as foreign) increases with chemical distance between their profiles (Sturgis & Gordon, 2012; Wittke et al., 2022). Since nestmate recognition and waterproofing rely on CHC classes with opposing properties, social insects may not be able to optimize both functions simultaneously. In environments where both are crucial, CHC composition likely reflects trade-offs.

Despite their ability to recognize foes, social insects remain vulnerable to invasion by closely related social parasites that mimic their CHC profiles (Lenoir et al., 2001a). Social parasitism has evolved several times independently in ants, accounting for up to one-third of all species in temperate zones (Kutter, 1969). Dulosis is a form of ant social parasitism where parasitic workers specialize in raiding allospecific host colonies to abduct their worker brood, whose social behaviour they later exploit as adults (D'Etorre & Heinze, 2001). While some dulotic species are facultative parasites, most are obligate and have lost essential abilities such as brood care and foraging. Their frequent and destructive raids, which peak during summer at high temperatures, exert strong selection on free-living host colonies, driving the evolution of defensive strategies (Brandt & Foitzik, 2004; Buschinger et al., 1980). Dulotic ants manipulate host behaviour and evade recognition through various chemical strategies, including chemical mimicry, which involves synthesizing chemical cues that resemble the host's profile, and chemical insignificance, characterized by the absence or reduction of recognition cues used by hosts to identify enemies. Parasites often engage in aggressive interactions with hosts during raids (Brandt et al., 2006; D'Etorre et al., 2002; Jongepier et al., 2015). When hosts encounter dulotic parasites, rapid recognition, and a collective defence are crucial to repel or escape the threat (Pamminger et al., 2011).

Our study focuses on the coevolving obligate dulotic social parasite *Temnothorax americanus* and its primary host *T. longispinosus* (Foitzik et al., 2001, 2009; Jongepier et al., 2014) for which the degree of escalation in their co-evolutionary arms race varies geographically (Foitzik et al., 2001). For instance, in regions with high parasite prevalence (PP), *T. americanus* carries fewer chemical recognition cues, facilitating its invasion into host colonies (Kaur et al., 2019; Kleeberg et al., 2017). Additionally, *T. americanus* secretes substances from its Dufour's gland that induce fights among host workers. This manipulative tactic, particularly common in parasites from high-prevalence areas, may enhance parasite success (Brandt et al., 2005; Jongepier et al., 2015). In response to parasite pressure, *T. longispinosus* populations alter their social colony structure (Herbers & Foitzik, 2002), shift their behavioural strategy from fighting to fleeing, and display increased aggression after enemy encounters (Jongepier et al., 2014; Kleeberg et al., 2014). Hosts also respond by increasing the diversity of chemical recognition cues between colonies in regions where parasites are present, potentially impairing the parasite's ability to match host profiles (Jongepier & Foitzik, 2016). Simultaneously, as ectotherms, their physiology and behaviour are strongly affected by temperature and humidity, which putatively impacts their interactions. For instance, *T. longispinosus* responds to drier conditions by a plastic increase of the proportion of *n*-alkanes in its CHC profile (Menzel et al., 2018). With potential trade-offs in functions of *n*-alkanes and recognition cues, impairment

in recognition abilities due to these dynamic shifts might be possible.

This study investigates how local climate and parasite pressure shape host–parasite interactions by influencing traits related to perception, signalling, and defence. In the colder, more humid northern regions with shorter seasons northern regions, we hypothesize that hosts, known for heightened aggression against conspecifics (Segev et al., 2017), will also exhibit stronger defences against parasites. As parasites prioritize quantity over quality when raiding host colonies (Miller, 2021), and the raiding period is shorter in colder climates, we expect parasites from these regions to exhibit more aggression to ensure that their raids are successful. In southern regions with warmer, drier climates, both species are expected to increase production of *n*-alkanes for desiccation resistance (Sprenger & Menzel, 2020), potentially conflicting with the host's need for methylated alkanes to recognize nestmates. To test these predictions, we analysed 10 populations (up to 1,000 km apart, Figure 1) across varying climates and PP, assessing behavioural interactions, CHCs, and colony structure.

Methods

Ant species, collection, and maintenance

Temnothorax longispinosus is a facultatively polygynous and seasonally polydomous ant (Foitzik et al., 2004; Herbers, 1986), with *Temnothorax* colonies typically reuniting in a shared nest during winter. Colonies are widely distributed in deciduous forests of northeastern North America and typically contain several dozen workers inhabiting preformed cavities in hollow acorns, sticks, or rock crevices on the forest floor (Herbers, 1989). It often occurs in sympatry with its related social parasite *T. americanus* (Foitzik et al., 2009), which conducts several raids during summer to abduct worker brood (Foitzik & Herbers, 2001; Foitzik et al., 2009). Parasite colonies are monogynous and sometimes polydomous, forming subunits capable of conducting independent raids (see Foitzik & Herbers, 2001). Each nest contains a few parasitic workers alongside captive hosts (Herbers & Foitzik, 2002). *Temnothorax americanus*, though capable of exploiting three different *Temnothorax* species, prefers *T. longispinosus* as a host, resulting in higher prevalences and colony sizes in high-density populations of this host (Brandt & Foitzik, 2004).

We collected ant colonies from July to September 2021, consisting of 5–250 host workers, during the peak raiding season. We collected at 10 locations in the northeastern USA, each separated by at least 100 km, typically over 200 km (Figure 1). Site selection was based on previous collection data, geographic location, and information on forest composition and density obtained from US Forest Service data. At each site, sampling occurred at 2–10 subsites within a 5-km radius to ensure reliable PP estimates while maintaining genetic homogeneity within populations and geographic isolation between them (Table S1, Jongepier et al., 2014; Kaur et al., 2019). Host colonies were collected at a minimum distance of 70 cm and had to contain at least one queen to maximize the likelihood of sampling independent colonies. We sampled parasite colonies regardless of distance but considered nests found within a 1-m vicinity, with either or both being queenless, to be polydomous. Upon collection, ant colonies were provisioned and transported under cooled conditions before being trans-

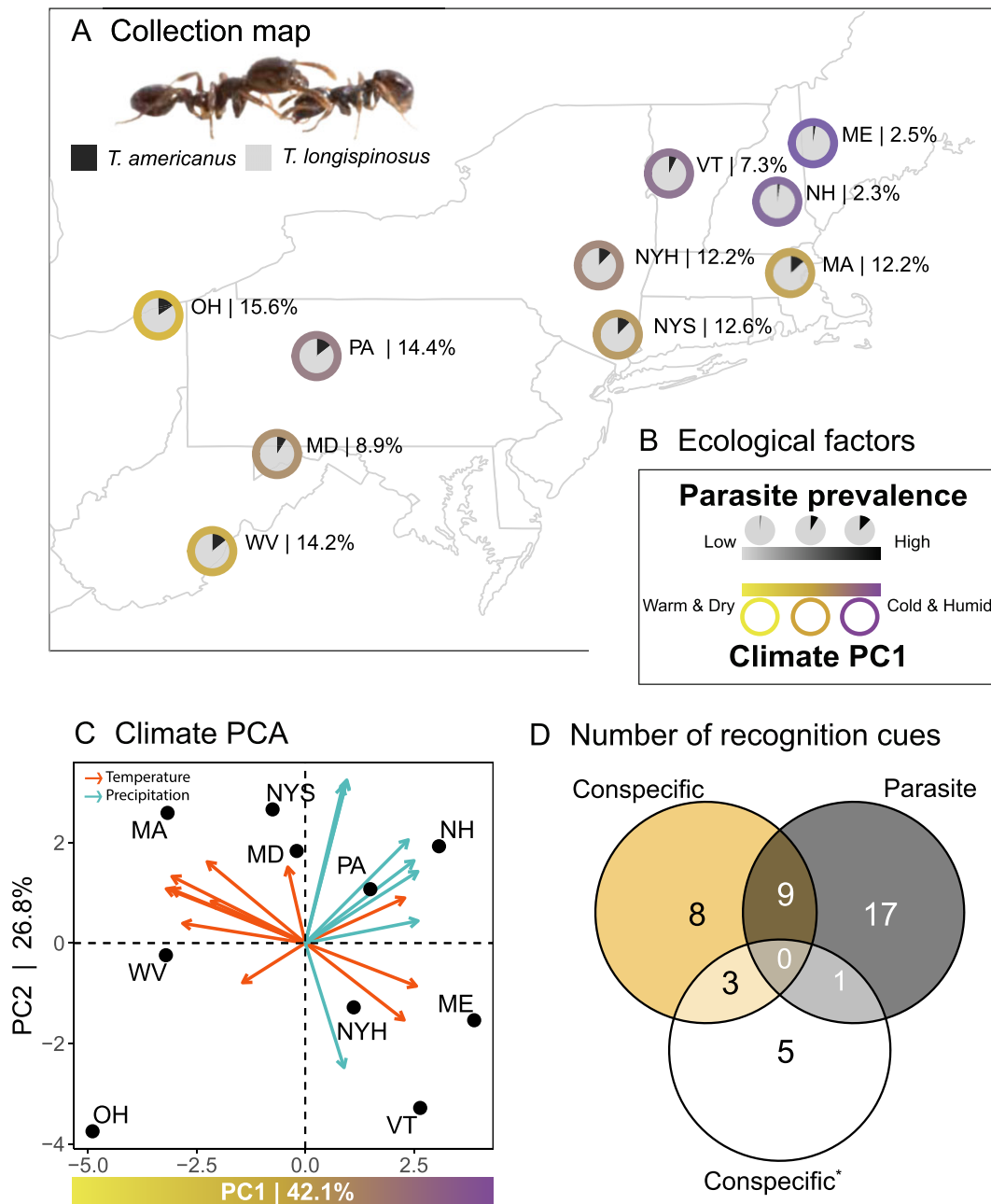


Figure 1. (A) Map of collection sites illustrating the geographical variation of the ecological factors found within legend box (B): parasite prevalence (% *Temnothorax americanus* colonies among host colonies) and climate variation indicated by PC1 climate values (determined by x-axis in C) (Table S1 for state abbreviations and population names, map adapted from Macit et al., 2024); Photo ©Romain Libbrecht. (C) Principal component analysis (PCA) used to characterize climate variation at study sites (Table S1). The arrows represent the contribution and direction of individual climate variables to the two principal components (PC1 and PC2) based on CHELSA bioclim variables (Karger et al., 2017; Macit et al., 2024), aligning populations from warm/dry climates on the left and cold/wet climates on the right. (D) Venn diagram comparing recognition cues (cuticular hydrocarbons linked to aggression) across studies. The open circle represents conspecific* recognition cues identified by Jongepier and Foitzik (2016) in *T. longispinosus*. Orange and black circles indicate recognition cues from this study associated with *T. longispinosus* aggression towards conspecifics and *T. americanus*, respectively.

ferred to artificial nest sites for acclimatization in the laboratory. Colonies were maintained in their natural composition, including all queens, workers, and brood. Each colony was housed in a three-chambered plastered nest box (10 × 10 cm), provided with a Bhatkar diet (Bhatkar & Whitcomb, 1970) and water ad libitum, and maintained under a 12 h:12 h light-dark photoperiod at 21 °C.

Parasite prevalence and climate

We estimated PP as the percentage of *T. americanus* colonies containing queens and/or workers within the pool of *T. americanus* and *T. longispinosus* colonies collected (Brandt & Foitzik, 2004; Foitzik et al., 2009; Jongepier et al., 2014). PP served as a proxy for parasite pressure on hosts and the ecological success of *T. americanus* (with an empirical

maximum of 15%–20%), as successful parasites are more likely to establish daughter colonies (Kaur et al., 2019). Given temporal and spatial variation in prevalence, we incorporated data from previous collections and sampled multiple sub-sites per population capturing stable geographic differences and a gradient in PP (Foitzik & Herbers, 2001; Herbers & Foitzik, 2002). This approach is biologically justified, as *Temnothorax* queens can have relatively long generation times, with maximum lifespans reported between 1.5 and 3 years and up to 7 years in rare cases (Beros et al., 2021; Plateaux, 1986). While detection is probabilistic, consistent patterns across years and regions support the reliability of our estimates. Indeed, a comparison across sampling time points indicates that the geographic variation in PP remained consistent over time (two-sided Wilcoxon signed rank test with continuity correction: $N = 7$, $V = 3$, $p = .08$). We use the same method as detailed in Macit et al. (2024) to calculate PP, incorporating multi-year data (Herbers & Foitzik, 2002; Jongepier et al., 2014; Kaur et al., 2019), which allowed us to calculate more reliable long-term prevalence estimates. To adjust these estimates for regions where *T. americanus* exploits several host species, we calculated PP based on the number of *T. americanus* colonies with *T. longispinosus* hosts divided by the total number of *T.* colonies (*T. longispinosus* + *T. americanus*), excluding those only containing *T. curvispinosus* host workers, a less preferred host (found in MA, NYS, OH, and WV; Table S1, Brandt & Foitzik, 2004). For parasite colonies with workers from both hosts, we applied a correction factor based on the ratio of *T. longispinosus* to *T. curvispinosus* exploited workers. For instance, a parasite nest containing equal numbers of both host species was counted as 0.5 rather than 1. This adjustment assumes that only half of the raids affected *T. longispinosus*, giving a more accurate estimate of parasite pressure on this species.

Climate also influences *Temnothorax* traits (Bengston & Dornhaus, 2014; Segev & Foitzik, 2019; Segev et al., 2017). We collected ants across a broad geographic range from Maine to West Virginia and obtained climate data from the CHELSA Bio-database (1981–2010, v. 2.1; Karger et al., 2017), which includes 10 temperature and 8 precipitation variables. A principal component analysis (PCA) was conducted, and climate-PC eigenvalues were used for further analyses based on previously published data (Macit et al., 2024). Principal component 1 (PC1) explained 42.1% of the variance and was associated with *T. americanus* prevalence, with higher prevalence linked to higher temperature and lower precipitation values (Pearson's correlation: $N = 10$, $r = -0.78$, $p = .008$). This suggests that the social parasite either prefers or performs better in warmer, drier climates, or that the host performs less well under these conditions. Additionally, the strong climate-prevalence link complicates independent analyses of their effects on trait expression (Macit et al., 2024).

Behavioural assays

On average, 155 host and 34 parasite colonies were collected per site to perform sympatric behavioural interactions under standardized conditions. From this collection, we tested the responses of 15 *T. longispinosus* colonies per population ($N = 150$) to the introduction of *T. longispinosus* and *T. americanus* workers originating from the same site 1-year post-collection (Table S2). Our approach contrasts with a previous study by Kaur et al. (2019), who used a full-factorial design,

involving fewer populations and including staged allopatric intrusions in which ant colonies were maintained for only a few weeks and tested in their natural colony demography. In our study, we kept colonies for over 1 year to ensure that most host workers had no prior experience with environmental conditions at their site of origin, including direct parasite interactions. A week before the assays, these *T. longispinosus* colonies were used to establish *T. longispinosus* standardized subcolonies ($N = 150$) comprising 10 workers, a queen (if present), five larvae, and a few eggs (details in supplementary material), placed in an arena. Trials consisted of the introduction of three types of sympatric workers in separate trials: *T. longispinosus* nestmates, *T. longispinosus* workers from sympatric colonies of the same pool involved in the experiments, and sympatric *T. americanus* workers. After 10 min of acclimation, a previously marked intruder was introduced with sterile forceps, and interactions were recorded for another 10 min (4K Sony FDR-AX33). Each day, 50 subcolonies underwent randomized trials, followed by a 1-week recovery period to control for prolonged physiological and behavioural shifts resulting from prior parasite encounters by *T. longispinosus* workers (Koenig & Moreau, 2024; Pamminer et al., 2011). Behavioural experiments were conducted three days per week, allowing all subcolonies to be observed within a 3-week period (Figure S1A). Each subcolony was randomly assigned an observation time of day, and this assignment remained consistent across the three trials. Observations took place from 8:30 to 16:30. Of the 450 recorded assays, 396 (nestmate: 134, conspecific: 138, parasite: 124; Table S9) were included in the behavioural analyses after excluding those with uncontrolled worker drift before recording or with fewer than five subcolony workers.

We analysed the behaviours of both the subcolony and intruders during their interactions. Each trial consisted of 27 scans sampled at 20-s intervals, covering a total of nine minutes. For each scan, we recorded the number of subcolony workers exhibiting specific behaviours, along with the behaviours of the intruders. For subsequent analyses, behavioural counts were summed across all scans to yield one total per behaviour per subcolony. Behaviours were then grouped into categories: aggressive behaviours included mandible opening, biting, stinging, pulling, dragging, carrying, and pinning (subcolony only), while sociopositive behaviours included antennation, grooming, and trophallaxis (Table S3). Additionally, we recorded brood-carrying behaviour, as a proxy for flight response for subcolonies (Jongepier et al., 2014), and passive behaviours (e.g., curled-up posture, immobility) in intruders, which were frequently observed. We performed beta-binomial generalized linear mixed models (GLMMs) with the *glmmTMB* package (Brooks et al., 2017) in R v.4.2.3 (R Core Team, 2024) with response variables being aggression, sociopositive, brood carrying or passive behaviour, respectively. We included as fixed effects intruder type, PP, climate (PC1), queen number, and the pairwise interactions of intruder type with PP, queen number, and climate, respectively (details in Supplement Tables S4 and S5). Additionally, we used the number of workers from the subcolony as fixed effect in the intruder response models to account for this source of variation. To limit model complexity and reduce overfitting, site variation was excluded. Potential pseudoreplication was addressed by including climate as a fixed factor to capture site-specific variation, and subcolony ID as well as intruder ID as random effects. Highly collinear factors,

which consisted mainly of the following fixed effects (i.e., PP, queen presence, and number of workers) and the interaction of these effects with the type of intruder (see [Table S4](#) for details), were sequentially removed by prioritizing the latter, and final models were selected via stepwise automatic reduction based on the Akaike information criterion ([Table S4](#)). Pairwise comparisons were adjusted using Bonferroni corrections.

CHC analyses

We analysed the CHC profiles of individual *T. americanus* ($N = 129$) workers and pairs of *T. longispinosus* nestmates ($N = 144$) from behavioural trial colonies (see “colony_collection.xlsx” in supplementary material). Workers were immersed in 350 μl hexane for 10 min, and extracts were concentrated under nitrogen flow. CHC analysis was conducted using a gas chromatograph (7890A, Agilent Technologies, USA) with a Zebtron Inferno ZB5-HT column (Phenomenex Ltd., Germany) and a mass selective detector (5975C, Agilent Technologies; details in the supplement). Substances were quantified via single-ion monitoring using MSD ChemStation (E.02.02.1431, Agilent Technologies). We considered hydrocarbons longer than C20, excluding non-hydrocarbons and compounds with an average proportion below 0.1% or a maximum relative abundance below 0.5%. Hydrocarbons were treated as functional traits ([Menzel et al., 2017](#)) and categorized as *n*-alkanes or methylated alkanes. Following [Jongepier and Foitzik \(2016\)](#), we identified CHC sets associated with colony aggression towards conspecifics ($N = 118$) and social parasites ($N = 105$). Using a stepwise reductive algorithm in R (based on [Wittke et al., 2022](#)), we identified CHCs whose quantity differences in the profile correlated with aggression, separately for conspecifics and parasites.

For each species, we performed permutational multivariate analyses of variance (PERMANOVAs) using the *adonis2* function from the *vegan* package ([Oksanen et al., 2022](#)) to examine links between the composition of overall CHC profiles, *n*-alkanes, or recognition cues, and PP or climate (PC1/2 eigenvalues). Ordinations of individual CHC profiles were done with non-metric multidimensional scaling (Bray–Curtis distances; package *vegan*). Associations between chemical composition and environmental factors were visualized using ordisurf (*vegan*). A PCA was conducted to link CHC relative abundance to climate and PP. To analyse intrapopulation variability in CHCs, *n*-alkanes, and recognition cues, we used the *betadisper* function (*vegan*). We then tested whether centroid values per species varied with climate and prevalence using Spearman’s rank correlations. Interspecific differences in the abundance of *n*-alkanes and recognition cues were analysed using beta GLMMs (*glmmTMB* package). Chemical distances between sympatric and allopatric host–parasite pairs were calculated using Bray–Curtis distances and assessed with a Mantel test (Pearson’s correlation, 2,000 permutations). Lastly, we examined how chemical distances among sympatric pairs varied along climate and PP gradients using Spearman’s rank correlation test.

Colony demographic analyses

Using generalized Poisson and quasibinomial GLMMs (*glmmTMB* package in R), we incorporated colony-level traits by including the number of individuals within a colony. Specifically, we counted the number of *T. longispinosus* queens and

workers in free-living colonies, the number of *T. americanus* workers in parasite colonies, and the proportion of *T. americanus* workers relative to the number of captive host and parasite workers in the colony. These variables were analysed in relation to climate and PP.

Results

Behaviour of subcolonies towards intruders

Temnothorax longispinosus workers were twice as likely to react aggressively to parasitic intruders as to foreign conspecifics, while aggression towards nestmates was rare (beta-binomial GLMM-intruder type: $N = 396$, $\chi^2 = 268.17$, $p < .001$; [Figure 2A](#)). Overall, aggression probability increased in colonies from colder/wetter climates (beta-binomial GLMM-climate: $N = 396$, $\chi^2 = 8.79$, $p < .01$; [Figure 2A](#)) and tended to be higher in those from high PP sites (beta-binomial GLMM-PP: $N = 396$, $\chi^2 = 2.88$, $p = .09$; [Figure 2A](#)). Workers picked up brood more frequently in response to social parasites than to conspecific intruders (beta-binomial GLMM-intruder type: $N = 396$, $\chi^2 = 75.96$, $p < .001$; [Figure 2B](#)), particularly in colonies from warmer/drier climates (beta-binomial GLMM-climate-intruder type interaction: $N = 396$, $\chi^2 = 6.57$, $p = .04$; [Figure 2B](#)). Sociopositive behaviours were most frequent towards nestmates and less common towards conspecifics or parasites (beta-binomial GLMM-intruder type: $N = 396$, $\chi^2 = 84.92$, $p < .0001$), with these behaviours remaining unaffected by environmental factors ([Table S6A](#)).

Behaviour of intruders towards subcolonies

Intruder aggression varied significantly by type, with conspecifics and social parasites reacting more aggressively than nestmates (beta-binomial GLMM-intruder type: $N = 396$, $\chi^2 = 35.65$, $p < .0001$; [Figure 2C](#)). Parasites from colder/wetter climates were less aggressive than those from warmer/drier regions (beta-binomial GLMM-climate-intruder type interaction: $N = 396$, $\chi^2 = 6.91$, $p = .03$; [Figure 2C](#)). Nestmates were the most active intruders, whereas conspecifics and social parasites remained passive in over half of the observations (beta-binomial GLMM-intruder type: $N = 396$, $\chi^2 = 102.80$, $p < .0001$; [Figure 2D](#)). Passivity increased in colder/wetter climates, particularly among parasites (beta-binomial GLMM-climate: $N = 396$, $\chi^2 = 7.22$, $p = .007$; climate-intruder type interaction: $N = 396$, $\chi^2 = 10.74$, $p = .005$; [Figure 2D](#)). Furthermore, parasites were the least likely to engage in sociopositive interactions with subcolony members, compared to nestmates and conspecifics (beta-binomial GLMM-intruder type: $N = 396$, $\chi^2 = 179.98$, $p < .0001$, [Figure S1C](#)). Sociopositive responses also decreased as subcolony size increased (beta-binomial GLMM-number of workers: $N = 396$, $\chi^2 = 4.56$, $p = .03$; [Figure S1B](#)). Only conspecifics showed a higher tendency for sociopositive responses in warmer/drier climates (beta-binomial GLMM-climate-intruder type interaction: $N = 396$, $\chi^2 = 5.72$, $p = .06$; [Figure S1C](#)).

Identification of recognition cues linked to host aggression

The chemical profiles of *T. longispinosus* contained 72 CHCs, 52 of which overlapped with the 63 CHCs found in *T. americanus* ([Figure S1D](#)). Using the reduced set of recognition cues, a strong positive correlation emerged between ag-

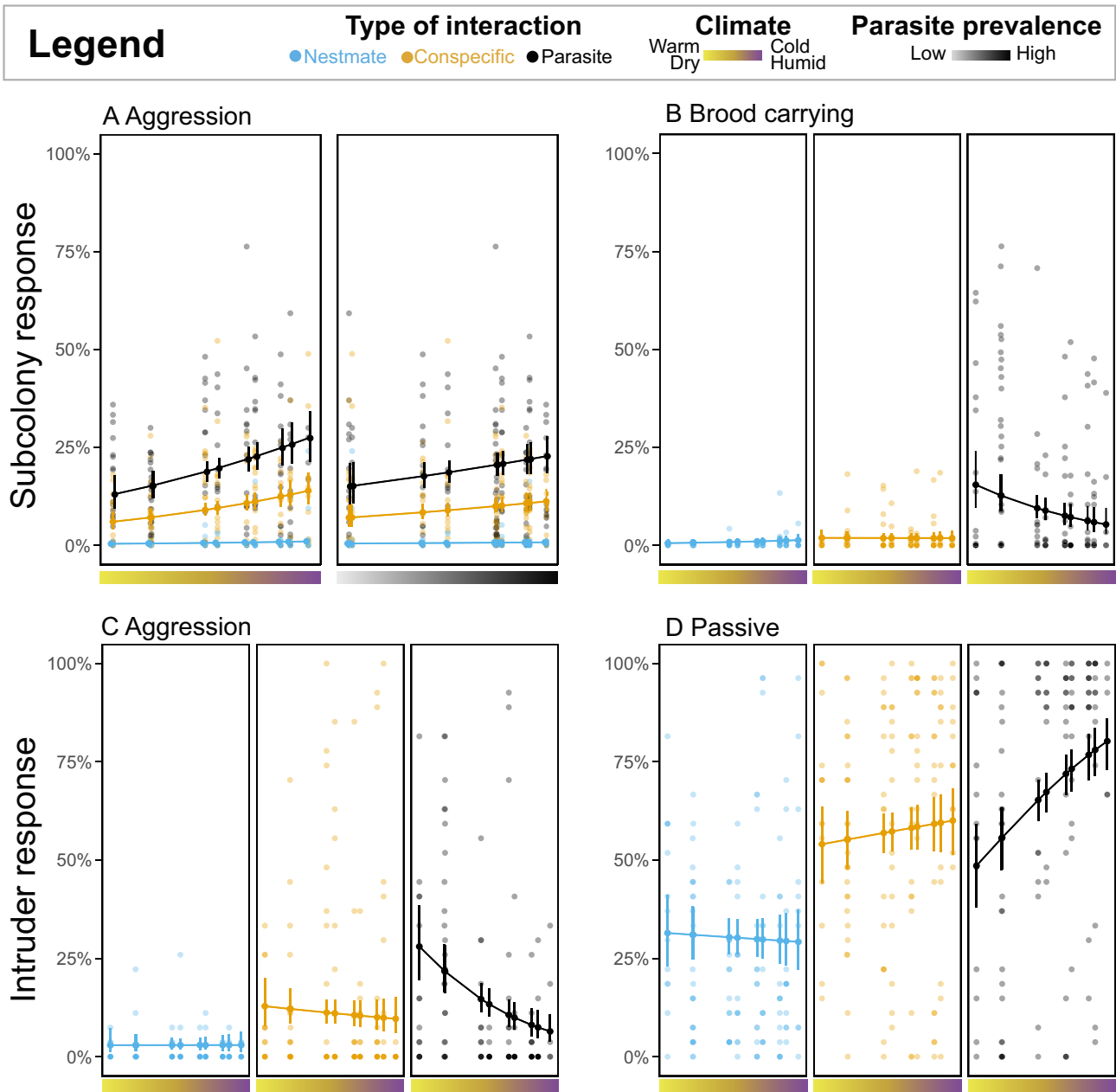


Figure 2. Scatterplots showing associations between climate, parasite prevalence, and behavioural responses of subcolonies towards each intruder type (A, B) and intruder responses towards subcolonies (C, D). Estimated marginal means are indicated by solid dots ($\pm 95\%$ CI), each connected by a line across the climate gradient. The other dots represent raw data. Interaction types are colour-coded based on the intruder type (blue: nestmate, orange: non-nestmate conspecific, black: parasite). Subplots are used where interaction with intruder type was detected (B, C, D). For each subplot, data appear to be arranged in columns since data points stem from 10 populations according to their climate value. PA and NYH share nearly identical climate values and therefore cannot be distinguished in the figure.

gression and chemical distance in both conspecific and parasite interactions (Spearman's rank correlations-conspecific: $N = 118$, $\rho = 0.45$, $p < .0001$; parasite: $N = 105$, $\rho = 0.54$, $p < .001$; Figure S4C, D), which was not detected when considering all CHCs (Spearman's rank correlations-conspecific: $N = 118$, $\rho = 0.15$, $p = .11$; parasite: $N = 105$, $\rho = 0.02$, $p = .81$; Figure S4A, B). Stepwise reduction identified 27 CHCs in *T. americanus* and 20 in *T. longispinosus* as recognition cues related to aggression in *T. longispinosus*, with nine compounds overlapping (Figure 1C). Three of these cues overlapped with those identified by Jongepier and Foitzik

(2016) for conspecific aggression (5-MeC27, 4-MeC28, and 5-MeC29), and one for parasite aggression (7-MeC31). None of the recognition cues were *n*-alkanes, despite these comprising 53% and 70% of the CHC relative abundance in *T. longispinosus* and *T. americanus*, respectively. All conspecific aggression cues were methylated alkanes, except for one alkene (C29-ene) found only in *T. longispinosus*. Seven of these were absent from *T. americanus* profiles (Figure S3). Similarly, all parasite recognition cues were methylated, with seven exclusively found in *T. longispinosus* and four in *T. americanus*.

Host and parasite CHC profiles and association to climate and parasite prevalence

Temnothorax longispinosus worker CHC composition was strongly linked to local climate but not PP (PERMANOVA-all CHCs-climate: $N = 144$, $df = 1$, $R^2 = 0.11$, $F = 17.04$, $p < .001$; PP: $N = 144$, $df = 1$, $R^2 = 0.007$, $F = 1.19$, $p = .27$; Figure 3A). Similar patterns were found for *n*-alkanes, conspecific, and parasite recognition cues, all of which were shaped by climate but unaffected by PP (PERMANOVA-*n*-alkanes-climate: $N = 144$, $df = 1$, $R^2 = 0.06$, $F = 8.47$, $p < .001$; PP: $N = 144$, $df = 1$, $R^2 = 0.005$, $F = 0.73$, $p = .44$; conspecific recognition cues-climate: $N = 144$, $df = 1$, $R^2 = 0.08$, $F = 12.55$, $p < .001$; PP: $N = 144$, $df = 1$, $R^2 = 0.006$, $F = 0.92$, $p = .49$, parasite recognition cues-climate: $N = 144$, $df = 1$, $R^2 = 0.10$, $F = 16.50$, $p < .001$; PP: $N = 144$, $df = 1$, $R^2 = 0.005$, $F = 0.81$, $p = .56$; Figure 3B, C, D). However, intercolonial variability in these CHC subsets was independent of both factors (Table S7).

In contrast, *T. americanus* CHC composition, particularly its *n*-alkane profile, tended to shift with PP but not with climate (PERMANOVA-all CHCs-climate: $N = 129$, $df = 1$, $R^2 = 0.01$, $F = 1.33$, $p = .22$; PP: $N = 129$, $df = 1$, $R^2 = 0.02$, $F = 2.28$, $p = .07$; *n*-alkanes-climate: $N = 129$, $df = 1$, $R^2 = 0.003$, $F = 0.36$, $p = .70$; PP: $N = 129$, $df = 1$, $R^2 = 0.05$, $F = 6.38$, $p < .01$; Figure 3E, F). However, recognition cue composition was unaffected by climate and PP (PERMANOVA-conspecific recognition cues-climate: $N = 129$, $df = 1$, $R^2 = 0.01$, $F = 1.32$, $p = .26$; PP: $N = 129$, $df = 1$, $R^2 = 0.01$, $F = 1.70$, $p = .13$; parasite recognition cues-climate: $N = 129$, $df = 1$, $R^2 = 0.01$, $F = 1.37$, $p = .19$; PP: $N = 129$, $df = 1$, $R^2 = 0.006$, $F = 0.79$, $p = .60$). Intercolonial variability in *T. americanus* *n*-alkanes was higher in southern sites with elevated PP and warmer, drier climates, whereas variability in conspecific recognition cues increased only with warmer and drier conditions (Spearman's rank correlations-*n*-alkanes-climate: $N = 10$, $\rho = -0.65$, $p = .05$; PP: $N = 10$, $\rho = 0.70$, $p = .03$; conspecific recognition cues-climate: $N = 10$, $\rho = -0.73$, $p = .02$; PP: $N = 10$, $\rho = 0.54$, $p = .11$; Figure 3G, H).

Temnothorax longispinosus chemical profiles contained a lower relative abundance of *n*-alkanes compared to *T. americanus* (beta GLMM-species: $N = 273$, $\chi^2 = 128.70$, $p < .0001$; Figure 4A). In *T. longispinosus*, *n*-alkane abundance decreased in warmer/drier climates, while *T. americanus* showed no climatic shifts (beta GLMM-species-climate interaction: $N = 273$, $\chi^2 = 3.67$, $p = .06$; Figure 4A). Additionally, *T. longispinosus* populations from cold/wet climates exhibited higher relative abundances of all seven *n*-alkanes and four of the five identified 3-monomethyl alkanes (Figure S2C). *Temnothorax longispinosus* profile contained more recognition cues related to conspecific and parasite aggression than *T. americanus* (beta GLMM-conspecific recognition cues-species: $N = 273$, $\chi^2 = 127.48$, $p < .0001$; parasite recognition cues-species: $N = 273$, $\chi^2 = 157.95$, $p < .0001$; Figure 4A, B). In both species, the relative abundance of recognition cues linked to conspecific and parasite aggression was higher in warmer/drier climates (beta GLMM-conspecific recognition cues-climate: $N = 273$, $\chi^2 = 3.90$, $p = .05$; parasite recognition cues-climate: $N = 273$, $\chi^2 = 5.59$, $p = .02$; Figure 4A, B). Moreover, parasite recognition cues tended to increase with PP in both species (beta

GLMM-parasite recognition cues-PP: $N = 273$, $\chi^2 = 3.70$, $p = .05$; Figure 4B).

Chemical distance between *T. americanus* and *T. longispinosus* sympatric and allopatric profiles

CHC distances between free-living hosts and parasites in sympatry and allopatry were similar (Pearson correlation: $N = 55$, $r = 0.09$, $p = .16$). However, sympatric host-parasite pairs from warmer/drier regions showed greater chemical divergence than those from cold/wet climates (Spearman rank correlation-climate: $N = 10$, $\rho = -0.79$, $p = .01$; Figure 4D). In contrast, chemical distance between sympatric hosts and parasites was unlinked to PP (Spearman's rank correlation-PP: $N = 10$, $\rho = 0.50$, $p = .14$).

Colony demography

Free-living *T. longispinosus* colonies in regions of high PP and a cold/wet climate contained more workers and queens (generalized Poisson GLMM-PP: workers: $N = 1566$, $\chi^2 = 30.09$, $p < .001$, Figure S5A; queens: $N = 1472$, $\chi^2 = 7.44$, $p < .01$, Figure S5B). Climate: workers: $N = 1566$, $\chi^2 = 19.07$, $p < .001$, Figure S1A; queens: $N = 1472$, $\chi^2 = 66.07$, $p < .0001$, Figure S5B). The number of *T. americanus* workers within parasite colonies increased with PP (generalized Poisson GLMM-PP: $N = 381$, $\chi^2 = 4.62$, $p = .03$, Figure S5C) but was unaffected by climate (Table S8). The proportion of *T. americanus* workers relative to captive host workers was unlinked to PP or climate (Table S8).

Discussion

Coevolutionary arms races between parasites and hosts are of great interest to evolutionary biology due to their reciprocal and continuous dynamics. It has been investigated through the study of biotic and abiotic effects on host-parasite coevolutionary dynamics (Byers, 2021; Johnson & Haas, 2021; Peacock et al., 2022), in particular in disease ecology (e.g., Gsell et al., 2023; Morales-Castilla et al., 2021). However, additional empirical data, especially from understudied systems such as brood or social parasites, are needed to clarify the underlying mechanisms. Climate, for example, has a major impact on insects, affecting their behaviour, physiology, and chemical profiles (Couper et al., 2024; Menges et al., 2024; Menzel et al., 2017). Our results show strong differences in various phenotypic traits associated with climate. As these differences persisted after 1 year under controlled laboratory conditions, this suggests that climate shapes host and parasite coevolutionary strategies. Geographical variation in behaviour indicates that parasites outperform hosts in warmer climates, potentially due to higher host availability and/or local adaptation to warm, dry environments. Additionally, our study reveals that climate and PP are differentially associated with host and parasite CHC profiles. Climate was linked to host CHC composition, while the parasite CHC profile was related to PP. Unexpectedly, hosts from warmer regions exhibited a lower proportion of *n*-alkanes and expressed more methylated alkanes, suggesting a trade-off between waterproofing and parasite detection in the CHC profiles. We identified recognition CHCs associated with host aggression towards parasites, including parasite-specific cues that may

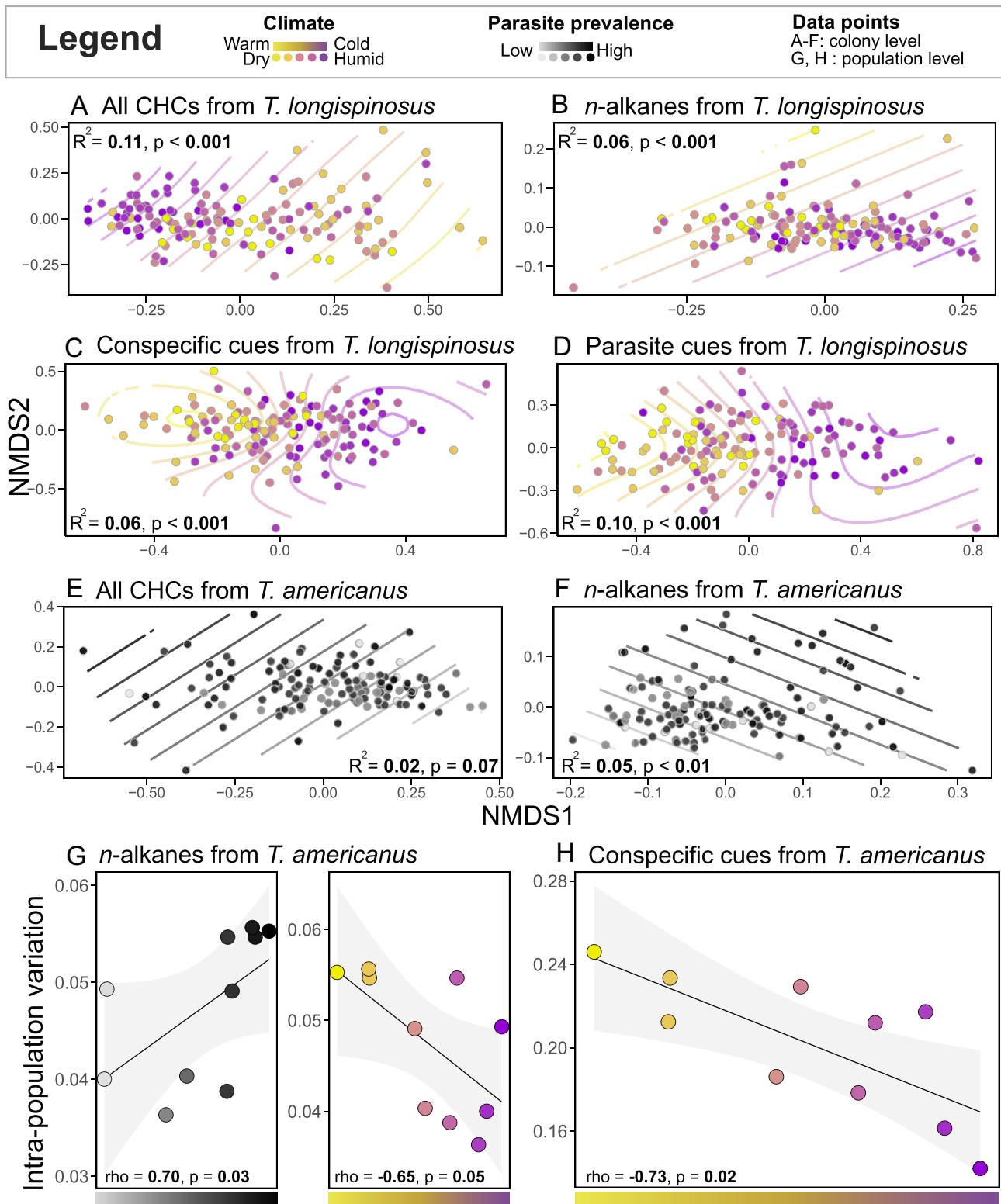


Figure 3. Non-metric multidimensional scaling (NMDS) plots showing permutational multivariate analyses of variance associations between colony cuticular hydrocarbon (CHC) composition, climate (colour-coded dots), and parasite prevalence (PP; greyscale contours). (A) All CHCs in *Temnothorax longispinosus*, (B) *n*-alkanes in *T. longispinosus*, (C) conspecific recognition cues in *T. longispinosus*, (D) *T. americanus* recognition cues in *T. longispinosus*, (E) all CHCs in *T. americanus*, and (F) *n*-alkanes in *T. americanus*. Contours indicate the linear (straight lines) or non-linear (curved lines) relationship between variation in chemical traits and environmental factors. (G) Scatterplot of mean *T. americanus* *n*-alkane variability (line \pm 95% CI), positively associated with PP but negatively with climate. (H) Scatterplot of mean variability (line \pm 95% CI) of recognition cue, used by *T. longispinosus* for conspecific recognition, found in *T. americanus*, in relation to climate.

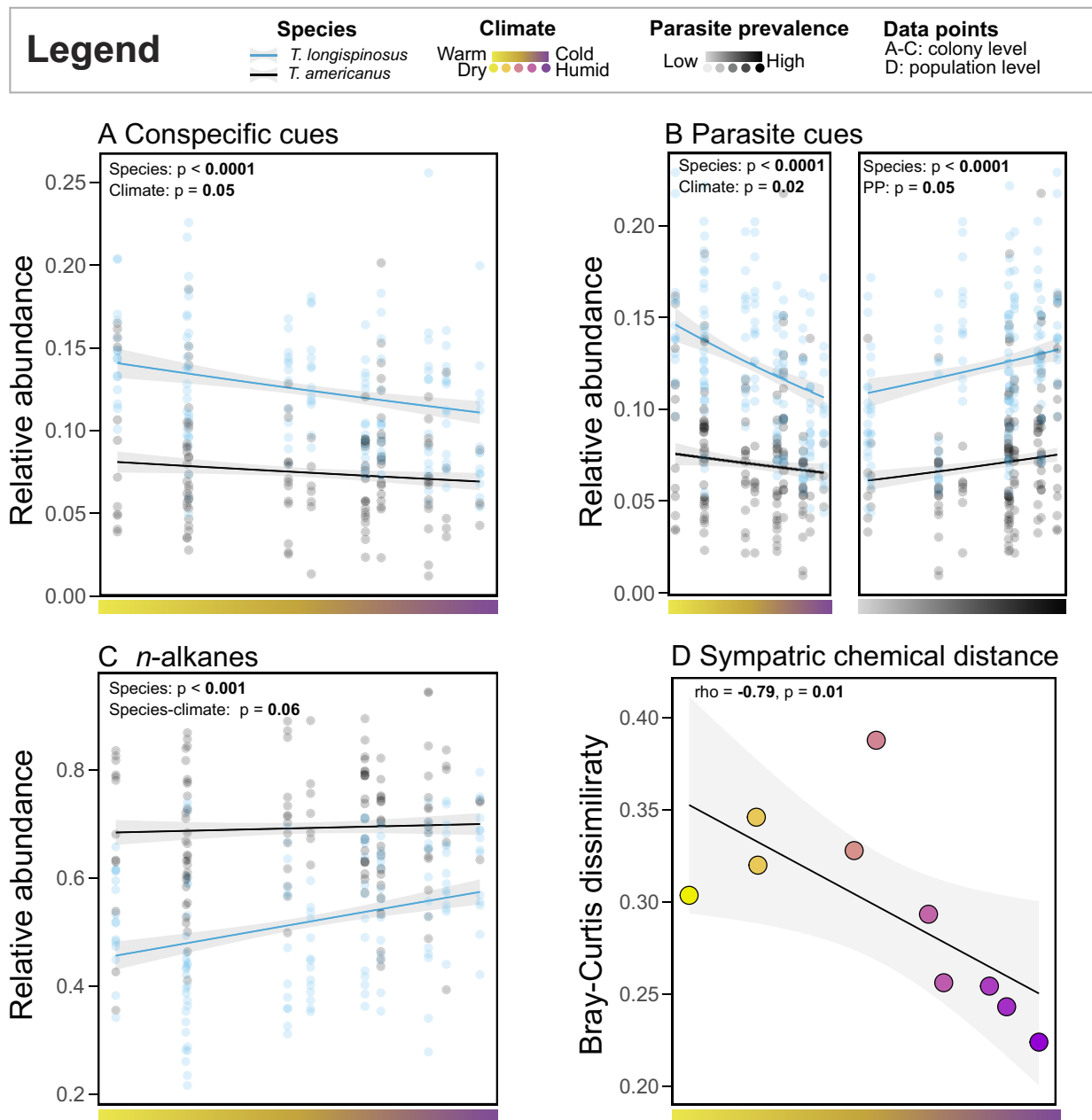


Figure 4. Scatterplots of estimated marginal mean relative abundances (line \pm 95% CI) of (A) conspecific recognition cues, (B) parasite recognition cues, and (C) *n*-alkanes in hosts (blue) and parasites (black) across climate gradients. (D) Scatterplot showing decreasing CHC profile mean dissimilarity (line \pm 95% CI) in sympatric host–parasite pairs along the climate gradient.

act as undesirable markers and *T. longispinosus*-specific cues that could function as desirable signals for nestmate recognition.

Influence of climate and parasite prevalence on behaviour

In this system, it has previously been shown that hosts exhibit behavioural, chemical, and morphological defences to prevent or minimize parasite attacks (Grüter et al., 2018; Jongepier et al., 2014). In *T. longispinosus*, workers primarily use collective aggression against parasitic intruders but shift to nest evacuation under increasing parasite pressure (Jongepier et al., 2014; Kleeberg et al., 2015; Segev et al., 2017). Here, we further investigated these dynamics by ex-

amining how climate and PP influence the behaviour of *T. longispinosus* and *T. americanus* during interactions. We hypothesized that hosts and parasites from colder and more humid northern regions exhibit higher aggression, as both may be under selection for more efficient resource acquisition and defence due to the shorter active season. Previous studies have shown that hosts from colder northern regions display increased aggression towards conspecifics (Segev et al., 2017), and that parasite decision-making during raids may be constrained by limited time (Miller, 2021). In line with this, hosts from colder climates displayed greater aggression, suggesting that abiotic factors primarily drive this behavioural trait rather than parasite pressure. For example, higher host aggression may evolve in environments with lower resource avail-

ability, such as shorter growing seasons, to protect limited resources like food and brood (Cristaldo et al., 2016; Sorvari & Hakkarainen, 2004). This aligns with seasonal aggression patterns in *Formica exsecta* and *Plagiolepis pygmaea* (Katznerke et al., 2006; Thurin & Aron, 2008) and reduced recognition abilities in *F. xerophila* at lower temperatures, leading to increased aggression (Tanner, 2009). In contrast, parasite workers from cold, wet climates were less aggressive and more passive during host colony invasions, potentially eliciting stronger defensive responses from the hosts. A cross-fostering study (Kaur et al., 2019) demonstrated that parasite behavioural and chemical strategies can influence host responses during intrusions, including brain gene expression. This indicates that parasites can modulate both host behaviour and neural activity. While parasite behaviour is typically shaped by selection for successful raiding, their reduced aggression in northern regions may reflect lower tolerance to colder and more humid climates. Although temperature was held constant in our experiments, the observed patterns may result from thermal mismatches between hosts and parasites, with parasites potentially exhibiting lower thermal limits that are exceeded by winter conditions in northern latitudes. Furthermore, cold winters at high latitudes might restrict parasite populations, and as a result limit prevalence, while summer heat in the South could enhance their aggressive behaviour (Bradshaw & Holzapfel, 2006). In terrestrial ectotherms, including ants, temperature strongly affects behavioural activity, with upper thermal limits showing little variation and lower limits decreasing with latitude (Sunday et al., 2010). Temperature-driven changes in metabolic activity may further influence behavioural interactions (Krapf et al., 2023; Menges et al., 2023). For example, in *T. curvispinosus*, a host of *T. americanus*, warmer winters have been shown to enhance running speed (Diamond et al., 2018), which could similarly increase raiding efficiency in the parasite.

We predicted that flight responses in the host, characterized by workers picking up larvae, as an essential defence behaviour during parasite invasion, would increase with parasite pressure (Jongepier et al., 2014). However, climate emerged as the primary predictor, with hosts from warmer regions displaying higher levels of this behaviour. Notably, flight responses increased in warmer climates while aggression decreased, suggesting that the host's collective defence strategies, ranging from fight to flight (Jongepier et al., 2014), may be shaped by local climatic conditions rather than PP.

Impact of climate and parasite prevalence on cuticular hydrocarbon trait expression

CHCs are essential for both waterproofing and recognition, but these functions rely on compounds with opposing biophysical properties, creating a potential trade-off. We analysed CHC composition and functional classes in relation to climate and PP. Our results confirm that parasites were chemically similar to their hosts but carried fewer methylated alkanes, consistent with previous studies (Kleeberg et al., 2017). In populations from warmer, drier climates, host and parasites showed greater chemical divergence, likely resulting in quick parasite discrimination and more effective nest evacuation (D'Ettore et al., 2002). While PP did not directly affect chemical distance, higher prevalence in these climates may drive hosts to increase the proportion of methylated alkanes. Greater divergence could also result from parasites adopting

generic chemical profiles to exploit multiple host species, as *T. curvispinosus* is also parasitized in warmer regions (Brandt et al., 2005).

In *T. americanus*, *n*-alkane composition was not associated with climate, suggesting either that the existing *n*-alkane profile is broadly suited to conditions across its range or that the species is genetically constrained and unable to adjust its profile to better tolerate cold climates. The high *n*-alkane levels may provide sufficient waterproofing while also aiding parasites in evading detection by diluting host recognition cues (Lorenzi & d'Ettore, 2020). Greater variability in *n*-alkane composition was observed in regions with high PP and warm, dry climates, possibly due to genetic diversity, host diversity, or microclimatic variation, which may hinder hosts from learning parasite CHC profiles. Contrary to expectations, PP did not affect *n*-alkane proportion but did influence composition as such, with unclear effects on host recognition.

In hosts, *n*-alkane composition varied with climate but in the opposite direction of expectations. The relative abundance of *n*-alkanes and monomethylated alkanes, both important for waterproofing, increased in colder, wetter climates, where desiccation risk is lower (Menzel et al., 2018; Wagner et al., 2001). This suggests an evolutionary trade-off, where hosts may prioritize recognition cues over waterproofing in warmer, drier regions if parasite pressure or other biotic pressures are high, potentially compromising optimal behavioural defence against parasites.

Ants have exceptional olfactory abilities crucial for distinguishing nestmates from foes (Sturgis & Gordon, 2012). Recognition relies on detecting either the presence of undesirable cues or the absence of desirable cues, or both (Guerrieri et al., 2009; Neupert et al., 2018; Sherman et al., 1997). In *T. longispinosus*, methylated alkanes play a key role in conspecific recognition, and their increased variability in parasite-exposed populations suggests a defensive function (Jongepier & Foitzik, 2016). This latter study therefore assumed that parasite recognition relied on the same compounds as conspecific recognition, but our findings suggest otherwise. We identified that host aggression towards conspecifics or parasites was primarily associated with a distinct set of methylated alkanes. Some of the cues related to parasite aggression were exclusively found on parasites, while others were unique to hosts. This suggests that hosts may recognize parasites by comparing both the presence and absence of specific compounds against their internal recognition template (Neupert et al., 2018).

The composition of parasite recognition cues carried by *T. longispinosus* was linked to climate. Both species exhibited higher recognition cue abundance in warmer climates, possibly to counter increased evaporation rates (Menzel et al., 2019). This was unexpected, as reliable recognition is crucial for detecting intruders. However, with limited knowledge of odour perception, it remains unclear how recognition templates evolve within a colony. In contrast, parasite recognition cue composition was unaffected by climate or PP, indicating minimal geographic variation. Parasites also had lower recognition cue abundance than hosts, which probably contributes to them not being detected.

Variation in colony size and social structure with climate and parasite prevalence

Our study found that climate and, to a lesser extent, PP had opposing effects on host colony structure: colonies from

colder, high-prevalence regions contained more queens and workers, in contrast to previous findings (Foitzik et al., 2009; Herbers & Foitzik, 2002). In regions of high parasite pressure, polygyny, especially when combined with polydomy, may function as a bet-hedging strategy to protect host colonies against raids, particularly by reducing the risk associated with queen loss. In colder climates, polygyny may also eliminate the risky independent founding phase (Bourke & Heinze, 1997), and larger colonies may enhance winter survival. *Temnothorax americanus* colonies also had more workers in high-prevalence regions (Herbers & Foitzik, 2002), which could potentially lead to larger colonies through a greater investment in reproductives. However, parasite colony size was unaffected by climate.

Conclusions

Abiotic factors play an important role in shaping coevolutionary interactions between hosts and parasites, but their complex and multifactorial effects require further investigation to elucidate the underlying mechanisms (Couper et al., 2024; Ragonese et al., 2024). Understanding the relationship between climate and host–parasite interactions is increasingly important for conservation, given recent dramatic declines in insect populations and the strong influence of abiotic factors on their physiology and behaviour (Franke et al., 2019; Ragonese et al., 2024). Our findings demonstrate that climatic conditions are closely linked to the geographic variation in host and parasite traits expressed during behavioural interactions, supporting growing evidence that climate is a key factor shaping host–parasite dynamics (Couper et al., 2024; Dziuba et al., 2023). This underscores the need to systematically incorporate abiotic factors into coevolutionary research.

Supplementary material

Supplementary material is available at *Journal of Evolutionary Biology* online.

Data availability

All data underlying the results of this study are available in Dryad at the following DOI: <https://doi.org/10.5061/dryad.qjq2bvqv2>.

Author contributions

Erwann Collin (Conceptualization [lead], Data curation [lead], Formal Analysis [lead], Investigation [lead], Methodology [lead], Project administration [lead], Resources [supporting], Supervision [supporting], Validation [equal], Visualization [lead], Writing – original draft [lead], Writing – review & editing [equal]), Maide Nesibe Macit (Conceptualization [equal], Formal Analysis [supporting], Methodology [lead], Project administration [lead], Software [supporting], Visualization [supporting], Writing – review & editing [equal]), Marti Wittke (Conceptualization [supporting], Formal Analysis [equal], Methodology [equal], Software [equal], Writing – review & editing [equal]), Chris Hörmann (Formal Analysis [supporting], Investigation [supporting], Writing – review & editing [supporting]), Claudio Haase (Formal Analysis [supporting], Investigation [supporting], Writing – review & editing [supporting]), Laura Heil (Formal Analy-

sis [supporting], Investigation [supporting], Writing – review & editing [supporting]), Maria Litto (Data curation [supporting], Project administration [supporting], Software [supporting]), Florian Menzel (Conceptualization [equal], Methodology [equal], Resources [equal], Writing – review & editing [equal]), Barbara Feldmeyer (Conceptualization [lead], Funding acquisition [lead], Methodology [lead], Project administration [lead], Supervision [lead], Writing – review & editing [equal]), and Susanne Foitzik (Conceptualization [lead], Investigation [supporting], Funding acquisition [lead], Methodology [lead], Project administration [lead], Supervision [lead], Writing – review & editing [lead])

Funding

This study was funded by the German Research Foundation (DFG) in a grant to Barbara Feldmeyer (FE 1333/3-3) and Susanne Foitzik (Fo298/17-3) and in GRK 2526/1—project no. 407023052. Erwann Collin received funding from the Huyck Preserve, New York.

Acknowledgments

We thank Jonas Wittig, Marcel Adrian Caminer, Sophie Späth, and Jennifer Lee Grossmann for their help in ant collection.

Conflicts of interest

The authors declare no conflict of interest.

Ethical statement

Ant collection permits were obtained from parks/preserves, or we asked private landowners for permission to collect ant colonies. Import and export licences are not required for the transport of our study species. We followed the guidelines of the Study of Animal Behaviour and the legal and institutional rules.

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Received March 13, 2025; revised July 30, 2025; accepted August 2, 2025

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