

Increased acclimation ability accompanies a thermal niche shift of a recent invasion

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Abstract

1. Globalization is removing dispersal barriers for the establishment of invasive species and enabling their spread to novel climates. New thermal environments in the invaded range will be particularly challenging for ectotherms, as their metabolism directly depends on environmental temperature. However, we know little about the role climatic niche shifts play in the invasion process, and the underlying physiological mechanisms.
2. We tested if a thermal niche shift accompanies an invasion, and if native and introduced populations differ in their ability to acclimate thermal limits.
3. We used an alien ant species—*Tapinoma magnum*—which recently started to spread across Europe. Using occurrence data and accompanying climatic variables, we measured the amount of overlap between thermal niches in the native and invaded range. We then experimentally tested the acclimation ability in native and introduced populations by incubating *T. magnum* at 18, 25 and 30°C. We measured upper and lower critical thermal limits after 7 and 21 days.
4. We found that *T. magnum* occupies a distinct thermal niche in its introduced range, which is on average 3.5°C colder than its native range. Critical thermal minimum did not differ between populations from the two ranges when colonies were maintained at 25 or 30°C, but did differ after colony acclimation at a lower temperature. We found twofold greater acclimation ability of introduced populations to lower temperatures, after prolonged incubation at 18°C.
5. Increased acclimation ability of lower thermal limits could explain the expansion of the realized thermal niche in the invaded range, and likely contributed to the spread of this species to cooler climates. Such thermal plasticity could be an important, yet so far understudied, factor underlying the expansion of invasive insects into novel climates.

KEYWORDS

acclimation, alien, climatic niche shift, ecophysiology, phenotypic plasticity, range expansion

1 | INTRODUCTION

Invasive species reduce biodiversity and disrupt ecosystem functioning (Bongaarts, 2019; Mack et al., 2000; Simberloff et al., 2013).

The spread of invasive species has been facilitated by globalization of trade and transport which introduce species beyond their native range (Chapman et al., 2017). Once introduced to a new habitat, a species needs to survive and reproduce before starting to spread

(Blackburn et al., 2011). Sometimes, new habitats present climatic conditions that are different from those in the species' native range (Hill et al., 2017; Kumar et al., 2015; Ørsted & Ørsted, 2019).

Yet, established invasive species are thought to conserve their niche in general, although studies assessing these climatic niche shifts have predominantly focused on plants (Guisan et al., 2014; Liu et al., 2020a; Petitpierre et al., 2012). Terrestrial ectotherms may have a higher capacity for colonization of new climates compared to endotherms (Liu et al., 2020a). Additionally, climatic niche shifts have been considered common in invasive insects (Bates et al., 2020; Hill et al., 2017), but studies report niche conservatism in key invasive insect species (Cunze et al., 2018; Roura-Pascual et al., 2006). Thus, it is unknown to what extent invasive insects succeed to establish under novel climates (Renault et al., 2018), that is, if they show a climatic niche shift between their native and invaded range. Also, the quantitative methods used to assess the climatic niche shifts do not reveal physiological differences of invasive populations.

A thermal niche shift could be particularly challenging for ectotherms, whose body temperature, and consequently metabolism and fitness, directly depends on the environmental temperature (Angilletta, 2009). Ectotherms, such as arthropods, can also locally adapt to novel climates to which they expand (Krehenwinkel et al., 2015; Lancaster et al., 2015). Local adaptation includes the evolution of a phenotype that increases performance and ultimately fitness in a set of local conditions (Kawecki & Ebert, 2004). But, a more rapid way to adjust to the environmental temperature changes would be thermal acclimation—a reversible physiological change which enhances performance (Angilletta, 2009). Unlike adaptation, acclimation is not heritable and phenotypic changes in adult workers, caused by temperature, are reversible. Here, we combine niche modelling with experimental approach to test if thermal plasticity underlies a climatic niche shift of an invasive insect.

We chose an invasive ant as a model system because ants are successful invaders with over 240 species established outside their native range (Bertelsmeier et al., 2017). There are several traits which facilitate their establishment like omnivory, polygyny and supercoloniality (Bertelsmeier et al., 2017; Holway et al., 2002). Most invasive ants are native to tropical and subtropical areas (Bertelsmeier et al., 2015), and as such are considered to be thermal specialists (Diamond & Chick, 2018). Because ant foraging ability and resource acquisition are directly governed by their thermal tolerance (Cerdá et al., 1998; Roeder et al., 2018), new thermal conditions are a key barrier ants need to overcome to establish in climatically distinct habitats.

To test if introduced populations can shift the thermal niche, and if this can be explained by differences in acclimation ability, we focused on *Tapinoma magnum*. This ant species had recently been introduced from its native range in North Africa to Europe (Seifert et al., 2017). Specifically, we asked three questions: (a) Does a thermal niche shift occur in the invaded range? (b) Do native and introduced populations differ in their critical thermal limits? (c) Do native and invasive populations differ in their acclimation ability? We predicted a niche shift between native and introduced ranges to be

accompanied by a greater ability to acclimate to lower temperatures in the introduced range, as cold tolerance is likely limiting the spread of this ant species to higher latitudes.

2 | MATERIALS AND METHODS

2.1 | Climatic and thermal niche analyses

To assess the difference in the climatic niche space between native and introduced populations, we used occurrence data points from our 17 sampling locations, combined with occurrence points from Seifert et al. (2017), which provides coordinates for 90 *T. magnum* colonies. We collected colonies at 17 sampling locations across native and introduced range (Figure 1) and brought them to the laboratory for acclimation experiments (see details below). To avoid errors due to spatial autocorrelation, nearest neighbour distance (NND) method was used to thin the data and occurrence points that were <0.05 units away from each other were removed (~5 km). After thinning, we had 18 occurrence points in the native and 62 in the invaded range (Figure 1). For each location, we extracted the 19 BIOCLIM variables from the WorldClim Global Climate Database at 2.5 arc minutes (~5 km) (Hijmans et al., 2005). These variables are frequently used in studies on climatic niches of species because they are biologically meaningful and publicly available (Peterson, 2011). They are derived from monthly temperature and rainfall values and represent annual trends (e.g. mean annual temperature, annual

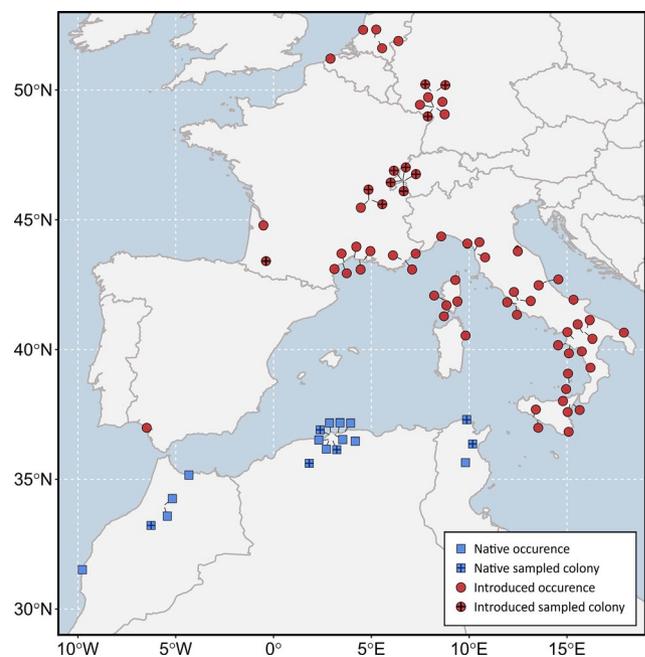


FIGURE 1 Distribution of the sampled *Tapinoma magnum* colonies across their native range in North Africa (blue squares) and introduced range in Europe (red circles). Six colonies were sampled in the native range: Morocco ($N = 1$), Tunisia ($N = 2$), Algeria ($N = 3$), and 11 in the introduced range: France ($N = 3$), Switzerland ($N = 5$), Germany ($N = 3$)

precipitation), seasonality (e.g. annual range in temperature and precipitation) and extreme or limiting climatic factors (e.g. temperature of the coldest and warmest months, and precipitations of the wet and dry quarters). Both analogous and non-analogous climates were considered in our analyses.

First, we tested for an overall climatic niche shift using all 19 BIOCLIM variables. We then analysed the thermal niche shift, using only temperature variables (BIO1–BIO11), as temperature variables are predicted to be more strongly correlated with ant thermal limits. We reduced these climate variables using a between-class analysis (BCA) with 'range' (invaded or native) as explanatory variable. BCA is a special case of a principal component analysis in which there is only one instrumental variable (Thioulouse et al., 2018). This analysis was done using the ADE4 package (Dray & Dufour, 2007). The resulting BCA axis was rescaled into 100×100 grid cells and converted into occurrence densities using the ECOSPAT package (Broennimann et al., 2012). To control for potential bias in the occurrence data, we calculated occurrence densities using kernel density smoothers, which smoothed potential gaps in the niche-space within a grid cell resulting in even density of occurrences for each grid cell (Broennimann et al., 2012). This allowed us to directly compare the environmental niche space in the native and invaded ranges.

2.2 | Niche comparisons

To determine the overlap of occurrence densities in the defined climatic niche space, we used Schoener's D (D) overlap (Schoener & Schoener, 1968; Warren et al., 2008). Schoener's D measures the overall match in occupied niche between the native and invaded range, spanning between 0 (no overlap) and 1 (complete overlap). To test whether the climatic niches in the native and invaded range are equivalent, we performed a niche equivalency test (Broennimann et al., 2012; Warren et al., 2008). We first pooled all occurrence points and randomly split them into two groups and calculated D overlap. We then repeated this 1,000 times to compare the distribution of simulated D overlaps to the observed D overlap. A D overlap below 95% of the simulated D overlap means the null hypothesis of niche equivalency is rejected. To examine the direction of niche shift, we calculated niche expansion, which is the percentage of the introduced niche that is not present in the native range. We also calculated unfilling—the percentage of native niche not present in the introduced range—and stability—the percentage of introduced niche shared with the native niche (Guisan et al., 2014).

2.3 | Acclimation experiments

We collected colonies from 17 different localities to test the acclimation ability of *Tapinoma magnum*. Six of our localities were from the native range in North Africa, and 11 colonies were collected

across their invaded range in Europe (Figure 1). Across the whole range, *T. magnum* consistently chooses to nest in disturbed areas close to buildings, roads, parking lots and in flower beds. However, North African colonies are small, monogynous and less abundant than European colonies (C. Lebas, field obs.). Even colonies in Mediterranean France and Italy have a strictly invasive phenotype where they dominate the landscape by creating polygynous and polydomous super colonies (C. Lebas, field obs.). We were conservative in our assignment of the native range to North Africa only, based on the behavioural differences observed between the continents, and the suggestion made by Seifert et al. (2017). *Tapinoma magnum* belongs to the *T. nigerrimum* complex that consists of four species. Three of those species have a supercolonial behaviour (workers from different nests are not mutually aggressive), and among them *T. magnum* shows the strongest invasive potential (Seifert et al., 2017). We assigned colonies to species based on worker morphology (Seifert et al., 2017). We confirmed identifications by typing three workers per colony at 11 diagnostic microsatellite markers: *Ant1368*, *Ant2794*, *Ant3648*, *Ant4155*, *Ant5035*, *Ant7249*, *Ant8424* and *Ant9218* (Butler et al., 2014), and *TM_3*, *TM_10* and *TM_16* (Zima et al., 2016). As reference samples, we used workers from all four species in the *T. nigerrimum* complex (*T. darioi*, *T. ibericum*, *T. nigerrimum* and *T. magnum*) that were previously identified by B. Seifert. The four species were detected as four different groups in STRUCTURE analyses (Pritchard et al., 2000), which allowed us to distinguish *T. magnum* from other species in the complex (Darras et al. in prep.). All colonies used in the experiments had pure *T. magnum* ancestry.

After collection, we kept our source colonies in the laboratory for at least 100 days at 25°C, 60% relative humidity (RH) and 12L:12D hr photoperiod ($M \pm SE$: 141 ± 7 days). These source colonies were used to create experimental colonies which were acclimated at 18°C or 30°C, 60% RH and 12L: 12D photoperiod for 21 days. Experimental colonies consisted of 100 workers placed in a plastic box (22 × 18 × 8 cm) lined with Fluon to prevent ants from escaping. We provided ants with an artificial nest consisting of a glass test tube (2 × 20 cm), half filled with water and sealed with cotton. We fed experimental colonies every 4 days with flies (*Calliphora vicina*), honey water and an agarose gel supplement containing vitamins, egg and honey (Bhatkar & Whitcomb, 1970). From each source colony, we created an experimental colony for each acclimation temperature. Exceptions were four colonies represented with two replicates for each acclimation temperature: one colony from Morocco and Switzerland, and two from France and Germany. In total, we incubated 23 experimental colonies at 18°C and 23 at 30°C, 7 from the native and 16 from the invaded range.

2.4 | Measuring critical thermal limits

Critical thermal limits (CTs) are temperatures at which animals lose muscle control (Lutterschmidt & Hutchison, 1997). To measure CTs, we used chilling/heating dry bath (Torrey Pines Scientific EchoTherm™

IC50; advertised accuracy $\pm 0.2^\circ\text{C}$) and a standardized protocol for recording ant thermal limits (Bujan, Roeder, Beurs, et al., 2020). In this dynamic protocol, five workers per colony are individually tested. Each worker is placed in a 1.5-ml microcentrifuge tube whose cap has been filled with cotton, to prevent the ants from hiding in the cap outside the heating block. Measuring critical thermal maximum (CT_{max}) trials starts at 36°C and temperature is increased by 2°C every 10 min. Before the temperature increase, each tube was inspected and rotated to determine whether ant lost muscle control, that is, loss of a righting response. We used the same procedure to measure CT_{min} but the trials started at 20°C and the temperature was lowered at 10-min intervals. We measured CTs for each colony at the beginning of the experiment, when all colonies were acclimated to 25°C , and after 7 and 21 days of experimental acclimation at 18 or 30°C . In total, we tested CT_{max} and CT_{min} of 1,088 workers. Ants are known to acclimate their critical thermal limits during a 7-day incubation (Chown et al., 2009; Clusella-Trullas et al., 2010; Jumbam et al., 2008). We used an additional 21-day incubation, as this period is sufficient for acclimation of ant traits related to thermal tolerance and desiccation resistance (Menzel et al., 2018).

2.5 | Analysing differences in critical thermal limits

We analysed the effects of acclimation temperature, incubation time and distribution range on CT_{max} and CT_{min} with generalized linear mixed-effect models (GLMMs). We used *lmer* function in the LMERTEST package (Kuznetsova et al., 2017) and included colony identity as a random factor. We performed the analyses separately for CT_{max} and CT_{min} at 18 and 30°C . We examined the country-level differences in CT_{min} at 18°C , as this treatment showed the strongest acclimation effect. To choose the optimal model, we compared Akaike Information Criterion (AIC) of GLMMs with a different number of fixed factors. In all cases, the optimal model was the complete model (Table S1). We tested the significance of model terms via pairwise comparisons using the package EMMEANS (Lenth et al., 2018). Because we observed a high mortality in colonies incubated at 18°C , we counted the number of live workers remaining after 21 days and compared the mortality rates observed in colonies originating from native and introduced ranges. All analyses were performed in R version 3.6.2 (R Core Team, 2019).

3 | RESULTS

3.1 | Climatic niche shifts

In the introduced range, *T. magnum* experiences a 3.5°C lower mean annual temperature compared to its native range (Native: $M \pm SE = 17.1 \pm 1.3^\circ\text{C}$, Invaded: $13.6 \pm 2.7^\circ\text{C}$). Minimum mean annual temperature is 4.2°C lower in the invaded range; however, maximum mean annual temperature is the same across both ranges (Native: 13.3 – 18.2°C , Invaded: 9.1 – 18.2°C). There was

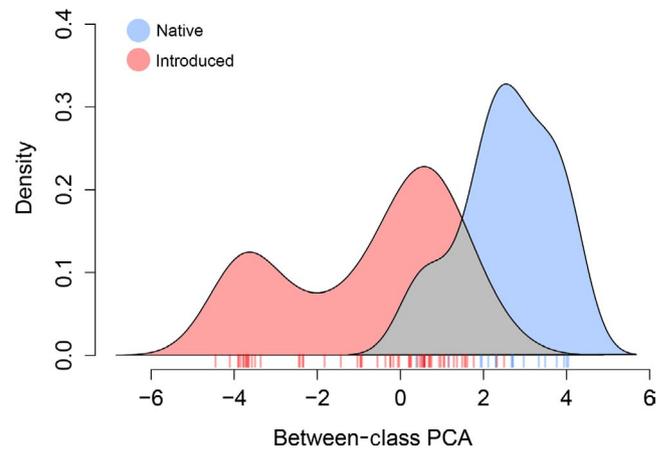


FIGURE 2 Density plot of observed occurrences between native and introduced range of *Tapinoma magnum* in between-class PCA space, reduced from 11 climate temperature variables

little overlap between the native and introduced thermal niches ($D = 0.33$), and niche equivalency was rejected ($p < 0.001$). The divergence between the two thermal niches was related to high expansion (52%), and relatively low unfilling (17%), while the stability between the two niches was 48% (Figure 2). When all climatic variables were considered, we observed equally low overlap among ranges ($D = 0.29$), and also rejected niche equivalency ($p < 0.001$; Figure S1).

3.2 | Thermal limits of the source colonies

After spending a minimum of 3 months in the laboratory acclimated at 25°C , critical thermal minimum of the source colonies did not differ between the native and invaded range (Figure 3; GLMM: $\beta = 0.62$, $SE = 0.49$, $z(90)$, $p = 0.23$). Critical thermal maximum was slightly higher in native populations (GLMM: $\beta = 0.60$, $SE = 0.23$, $z(90)$, $p = 0.024$), but this difference was only 0.5°C . The effect of colony, as a random factor, was significantly contributing to the CT_{min} optimal model ($p = 0.0007$), but not CT_{max} ($p = 0.67$).

3.3 | Acclimation of CT_{min}

After a 7-day incubation at 18°C , colonies from both native and invaded range lowered their CT_{min} (Figure 4; Table S1). This trend did not continue in native colonies while the introduced colonies tolerated on average $-1.4 \pm 0.1^\circ\text{C}$ ($M \pm SE$) after 21 days of incubation. This temperature was 2.9°C lower than at the beginning of the experiment and two times lower than the decrease recorded in native colonies after 21 days. Significant CT_{min} decrease with prolonged incubation was consistent across colonies from all countries within the invaded range (Table S2; Figure S2). In native colonies, 71% of the workers died after 21 days of incubation at 18°C which was 2.4 times higher mortality than in colonies from the invaded range ($\chi^2 = 8.8$, $df = 2$, $p < 0.002$). Incubation at 30°C did not alter CT_{min}

FIGURE 3 Critical thermal limits of native and introduced colonies after spending a minimum of 3 months in the laboratory at 25°C: (a) mean critical thermal maximum (CT_{max}) and (b) mean critical thermal minimum (CT_{min}). The error bars are showing $\pm SE$

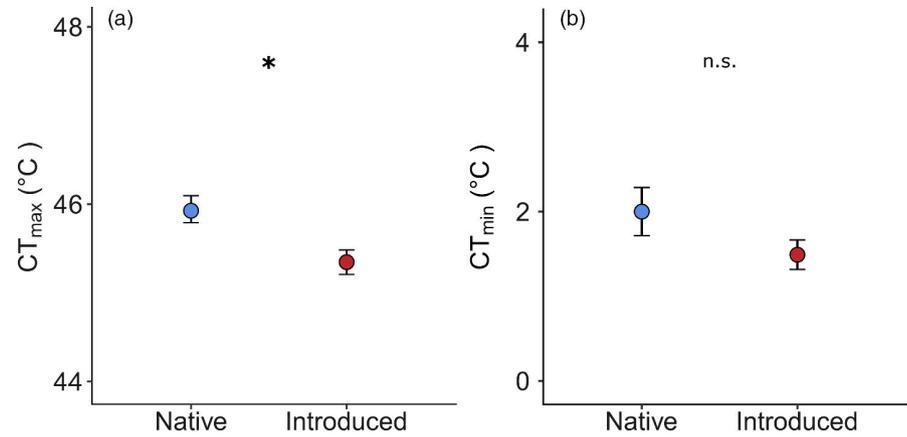
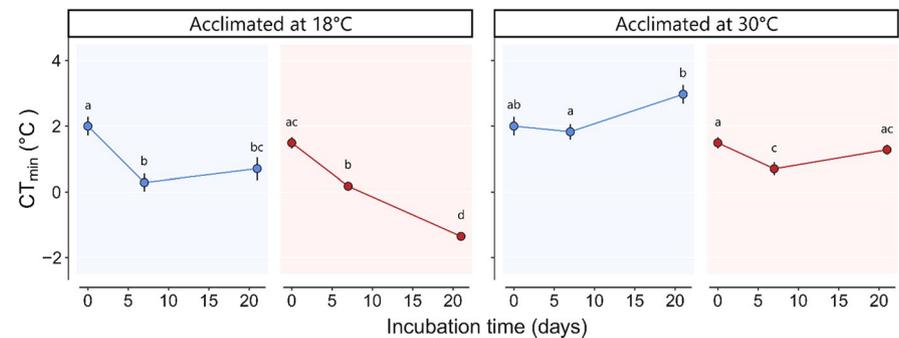


FIGURE 4 Mean critical thermal minimum (CT_{min}) after incubation time of 7 and 21 days at 18°C, and 30°C. Colonies from the native range are shown in blue, and introduced range in red panels. The error bars are showing $\pm SE$



of introduced colonies while native colonies show a slight increase in CT_{min} after 21 days (Figure 4; Table S1).

3.4 | Acclimation of CT_{max}

There was no marked change in CT_{max} at 18°C across the native and introduced populations throughout the 21-day incubation period (Figure S3a; Table S1). At 30°C, ants from both native and introduced populations had a significantly higher CT_{max} after 7 days (Figure S3b). During this time, CT_{max} of native populations increased for 1.4°C, and we observed a similar increase of 1.0°C in introduced populations. After 21 days, introduced populations maintained this elevated CT_{max} while native populations decreased their CT_{max} (Figure S3b; Table S1).

4 | DISCUSSION

Using a combination of niche shift analysis and acclimation experiments, we found that a recent introduction into colder climates resulted in a realized thermal niche shift, accompanied by higher acclimation ability of CT_{min} . Such thermal plasticity was recorded in some invasive populations of amphibians (Winwood-Smith et al., 2015), and insects (Nyamukondiwa et al., 2010), including ants (Coulin et al., 2019). But here we show that higher acclimation ability accompanies a climatic niche shift in the invaded range, using a quantitative analysis of niche equivalency, expansion and unfilling.

We found that prolonged exposure to low temperatures results in higher acclimation ability of CT_{min} and higher survival in introduced populations. Considering the ability of introduced populations of *T. magnum* to decrease CT_{min} without high mortality costs, the acclimation capacity of introduced populations is likely contributing to their invasive success due to greater fitness in colder climates.

Our findings that a cooler climate promotes acclimation ability of CT_{min} offers one of the mechanisms for ectotherm expansion to novel climates. Climatic niche shift studies usually focus on the presence of the shifts based on occurrence data (Broennimann et al., 2007; Hill et al., 2017; Li et al., 2014; Ørsted & Ørsted, 2019) while the mechanisms behind niche shifts are rarely tested (Hill et al., 2013; Krehenwinkel et al., 2015; Li et al., 2014). For example, a realized niche shift was observed in another invasive ant—*Nylanderia fulva*—but the mechanism behind it was not examined (Kumar et al., 2015). Realized niche shifts can occur after removing biotic or dispersal constraints present in the native range by human-mediated movement to the invaded range (Bolnick et al., 2010; Brooks et al., 2012; Keane & Crawley, 2002). In that case, the species is filling its fundamental niche, which was constrained in its native range. But the expansion of the realized niche can also be enabled by adaptive thermal plasticity (Kolbe et al., 2012; Lancaster et al., 2015). While adaptation of thermal tolerance can occur after species establishment under novel climatic conditions (Krehenwinkel et al., 2015; Sotka et al., 2018), we find this an unlikely scenario for *T. magnum*. We did not find differences in critical thermal minimum across the ranges, after an extended period in the laboratory (>3 months, Figure 3). This suggests that introduced populations maintained the thermal adaptations from

the native range and are not locally pre-adapted to the novel climatic conditions.

We found low acclimation ability of CT_{max} across native and invaded range, in both acclimation treatments. This is in accordance with other studies showing that upper thermal limits of insects are less variable than lower thermal limits (Addo-Bediako et al., 2000; Hoffmann et al., 2013), including in ants (Bishop et al., 2017; Bujan, Roeder, Beurs, et al., 2020). Moreover, acclimation of CT_{min} is common in insects (Gaston & Chown, 1999; Hu & Appel, 2004; Klok & Chown, 2003; Terblanche et al., 2006). Acclimation ability of CT_{min} was not a unique feature of our introduced populations. We found that across all native populations, a short-term exposure to 18°C resulted in lower CT_{min} (Figure S4). This might suggest an innate ability of *T. magnum* to acclimate to low temperatures and expand its realized niche. But longer exposures to lower temperatures resulted in high mortality in native colonies. As CT_{min} of native populations was the same after 7-day and 21-day incubation at 18°C it is unlikely that high mortality in native colonies selected for workers with a higher acclimation potential. Additionally, in both ranges, maximum mean annual temperature is 18°C, so this acclimation temperature was not expected to be detrimental.

Tapinoma magnum was introduced from a hot and dry Mediterranean climate to, on average, 3.5°C cooler habitats in Europe, so there is a greater selective pressure on CT_{min} . Thus, acclimation to cooler temperatures would be beneficial in the invaded range allowing for an earlier onset of foraging and food acquisition. Higher acclimation ability in CT_{min} observed in the invaded range could be an adaptation of the founder populations, or developmental and acquired in-situ in cooler climates of the invaded range. To test these hypotheses, a common garden experiment would be necessary, ideally over multiple generations (Bertelsmeier & Keller, 2018; Colautti & Lau, 2015).

Our results show that the ability to withstand lower temperatures corresponds to the climatic and thermal niche shifts, likely facilitating the spread of *T. magnum* to novel climates. Because invasive ants have a strong negative impact on native animal and plant communities, and ecosystem processes (Lach & Hooper-Bùi, 2009; Ness & Bronstein, 2004; Porter & Savignano, 1990), the extent of acclimation ability in other invasive ants is important. Particularly for 19 ant species which are listed among the 360 most invasive animals (www.iucngisd.org) by the International Union for Conservation of Nature (IUCN), because of their negative impact on biodiversity, human health and economy. We know that at least three of those 19 ant species show some ability to acclimate (Bujan, Roeder, Yanoviak, et al., 2020; Coulin et al., 2019; Jumbam et al., 2008).

Species distribution models predict future species spread based on current species distributions while assuming climatic niche conservatism (Bertelsmeier et al., 2015). However, models, which are calibrated using data from the native range only, have been shown to be poor predictors of the species' introduced range (Capinha et al., 2018). This model transferability is particularly limited in terrestrial ectotherms (Liu et al., 2020b). Additionally, if many species hold a strong acclimation capacity, which allows for a climatic niche

shift, then predictions of future distributions solely based on occurrence data will not be accurate. This is of particular importance for newly invasive species such as *T. magnum*, which are likely to continue their northern spread, and have significant impacts on native communities (Seifert et al., 2017). The data on acclimation ability of invasive species can help us better predict the likelihood of their establishment and define areas most vulnerable to invasion. Complementing computational analyses of climatic niche shifts with experimental studies could help us elucidate the drivers of invasions in a changing climate.

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AUTHORS' CONTRIBUTIONS

J.B., C.B., O.K.B. and J.G. conceived the ideas and designed methodology; J.G. and C.L. conducted the field collecting; E.C. and J.B. performed the acclimation experiments and collected the data on thermal limits; J.B. and O.K.B. analysed the data; H.D. performed the microsatellite sequencing and molecular ant identification; J.B., O.K.B. and C.B. wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at <https://doi.org/10.6084/m9.figshare.12847151> Bujan, Charavel et al (2020).

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