

Critical thermal limits and temperature-dependent walking speed may mediate coexistence between the native winter ant (*Prenolepis imparis*) and the invasive Argentine ant (*Linepithema humile*)

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ABSTRACT

Comparing the thermal tolerance and performance of native and invasive species from varying climatic origins may explain why some native and invasive species can coexist. We compared the thermal niches of an invasive and native ant species. The Argentine ant (*Linepithema humile*) is an invasive species that has spread to Mediterranean climates worldwide, where it is associated with losses in native arthropod biodiversity. In northern California, long-term surveys of ant biodiversity have shown that the winter ant (*Prenolepis imparis*) is the native species best able to coexist with Argentine ants. Both species tend hemipteran scales for food, and previous research suggests that these species' coexistence may depend on seasonal partitioning: winter ants are active primarily in the colder winter months, while Argentine ants are active primarily in the warmer months in northern California.

We investigated the physiological basis of seasonal partitioning in Argentine and winter ants by a) measuring critical thermal limits, and b) comparing how ant walking speed varies with temperature. While both species had similar CTmax values, we found differences between the two species' critical thermal minima that may allow winter ants to remain functional at ecologically relevant temperatures between 0 and 2.5 °C. We also found that winter ants' walking speeds are significantly less temperature-dependent than those of Argentine ants. Winter ants walk faster than Argentine ants at low temperatures, which may allow the winter ants to remain active and forage at lower winter temperatures. These results suggest that partitioning based on differences in temperature tolerance promotes the winter ant's continued occupation of areas invaded by the Argentine ant.

1. Introduction

Comparing the thermal tolerance and performance of native and invasive ectotherms from varying climatic origins may explain why some native and invasive species can coexist (Bujan et al., 2020; Kelley, 2014). The climate variability hypothesis (Angilletta, 2009; Gaston and Chown, 1999; Janzen, 1967) predicts that variable climates select for organisms with a broad fundamental thermal niche, while stable climates select for organisms with a narrow fundamental thermal niche. Research on thermal physiology across climatic gradients in terrestrial taxa and freshwater aquatic insects lends support to this hypothesis (Deutsch et al., 2008; Shah et al., 2017). The climate variability hypothesis has mostly been tested in the context of climate change (Deutsch et al., 2008; Shah et al., 2017). The climate variability hypothesis suggests that a species native to a climate with a broad thermal

range, such as the temperate zone, may be able to coexist with an invasive species from a climate with a narrower thermal range, such as the tropics (Molina-Montenegro and Naya, 2012). A native species in competition with an invasive species may persist if the native species can occupy a different niche from the invasive species (Culbertson and Herrmann, 2019; Jackson et al., 2016; Mori et al., 2019).

Ectotherms provide an ideal system for examining how changes in thermal physiology may mediate coexistence, since their body temperatures directly reflect external environmental conditions (Angilletta, 2009). Temperature-dependent physiological processes drive ectotherm metabolism, growth, development, and movement (Grigaltchik et al., 2012; Sinclair et al., 2016). Metabolic and thermal physiological processes can predict temperature-dependent foraging activity in ants (Prather et al., 2018).

Ant walking speed is strongly temperature dependent, likely due to

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the physiological properties of ectotherms (summarized in Hurlbert et al., 2008). Walking speed in ants can influence foraging outcomes: if ants walk faster, they can increase their total search area or make an increased number of trips to and from a food source in a given duration (Fewell, 1988). Walking speed may vary across the range of temperatures that a species can tolerate. For example, ants may forage extremely slowly at the cold end of their species' thermal limit.

The Argentine ant (*Linepithema humile*) is an invasive species found globally in Mediterranean and subtropical regions. It is native to southern Paraguay and northeastern Argentina (Roura-Pascual et al., 2004), an area with a relatively narrow thermal range. When established in the exotic range, Argentine ants decrease the diversity of native arthropods including native ants (Human and Gordon, 1996, 1997; Tillberg et al., 2007), plants (Bond and Slingsby, 1984), and vertebrates (Holway et al., 2002). The winter ant (*Prenolepis imparis*), which is native to temperate North America, appears to be the epigaic native ant species best able to coexist with the Argentine ant in parts of northern and southern California (Couper et al., 2021; Fitzgerald and Gordon, 2012; Gordon and Heller, 2014; Suarez et al., 1998). Both winter ants and Argentine ants tend hemipteran insects, and thus compete for food in the form of honeydew (Nygard et al., 2008).

Differences in thermal niches between winter ants and Argentine ants may explain why these two species coexist in California (Suarez et al., 1998; Ward, 1987). In 2017, the hottest average monthly temperature in northeastern Argentina was 24 °C in January, and the coldest monthly average temperature was 11 °C in June ("Córdoba, Córdoba, Argentina Weather History," 2022). By contrast, parts of the winter ant's native range in midwestern North America experienced a much wider range of monthly temperature averages in 2017, between -2 °C in December and 24 °C in July ("Chicago, IL Weather History," 2022). Our study site experienced similar yearly temperature variability to northeastern Argentina with a hottest average monthly temperature of 22 °C and a coldest average monthly temperature of 10 °C ("San Jose, CA Weather History," 2022). The climate variability hypothesis predicts that winter ants have a broader range of thermal tolerance than Argentine ants because they originate from more temperate and variable climates. Winter ants are active primarily in colder months in northern California (MacArthur-Waltz et al., 2021), while Argentine ants are the most active in summer and retreat to winter aggregations in colder months, where they continue to forage but over a more limited spatial

extent (Burford et al., 2018). In fall, winter, and spring (e.g. October–May), both species are actively foraging in northern California (MacArthur-Waltz et al., 2021; Burford et al., 2018).

We investigated thermal tolerance and performance between Argentine and winter ants. We asked the following questions: (1) Do Argentine ants and winter ants differ in their critical thermal limits (CTmax and CTmin)? (2) Is walking speed in Argentine ants and winter ants differentially affected by temperature?

2. Methods

To determine CTmax and CTmin for winter and Argentine ants, we collected workers of each species from 6 colonies (6 colonies/species, Table 1) on the Stanford University campus (Stanford, California, United States). All Argentine ant collection sites were separated by at least 500m to ensure that they represented separate colonies (Heller et al., 2008). Winter ant collection sites were separated by only ~30m; we assumed they represented separate colonies because colonies have been reported to be relatively small and to be organized around a single vertical tunnel (Tschinkel, 1987). In many cases, we were able to observe foraging trails on trees descending into these vertical nest tunnels within 2m of the base of the tree. At all sites, we collected ants from active foraging trails using handheld aspirators. We recorded air temperature (Hanna Instruments 9063 Portable Waterproof Microprocessor K-type Thermocouple Thermometer, Hanna Instruments Italia, Italy) and tree surface temperature (Ryobi ZRIR001 Non-Contact Infrared Thermometer, Solar Wide Industrial Ltd., Hong Kong) at all collection sites. Air temperatures were measured at ~1.5 m off the ground. After collection, but before thermal trials, we kept ants at room temperature (20–25 °C) in the lab for ~30 min to standardize short term temperature effects across warmer and colder collection days (Jayatilaka et al., 2011; Penick et al., 2017). All ant collections were made during the same time of year during winter (January–March) and during the afternoon (between 1 p.m.–5 p.m.) to minimize seasonal and daily effects.

To measure ants' CTmax temperatures, we placed individual workers into 200 μ L tubes with small ventilation holes in the cap. We placed vials containing ants into a PCR thermocycler (Eppendorf Mastercycler, Eppendorf, Germany) at room temperature (25 °C). We increased the temperature by 1 °C every 5 min up to 45 °C (Penick et al., 2017). We left the top of the thermocycler open at all times to allow observation. We

Table 1

Colony locations for winter and Argentine ants, collection dates, ambient air temperature (degrees Celsius) during collection, and sample sizes of number of ants per colony used for CTmax and CTmin trials. NA is listed if a colony was not sampled.

Colony_ID	Species	Latitude/Longitude	Date of Collection	Ambient Air Temperature During Collection	Sample Size
Colony 561	Winter ant	37.43790, -122.16711	CTmin: 3-18-17 CTmax: 1-28-17	CTmin: 21.2 CTmax: 16.0	CTmin: 7 CTmax: 8
Colony 562	Winter ant	37.43796, -122.16728	CTmin: 3-18-17 CTmax: 1-28-17	CTmin: 21.9 CTmax: 15.5	CTmin: 7 CTmax: 8
Colony 563	Winter ant	37.43807, -122.16743	CTmin: 3-18-17 CTmax: 1-28-17	CTmin: 22.5 CTmax: 15.4	CTmin: 7 CTmax: 8
Colony 551	Winter ant	37.43772, -122.16764	CTmin: 3-18-17 CTmax: 1-28-17	CTmin: 22.5 CTmax: 15.5	CTmin: 7 CTmax: 8
Colony 688	Winter ant	37.43749, -122.16802	CTmin: NA CTmax: 1-28-17	CTmin: NA CTmax: 15.7	CTmin: NA CTmax: 7
Colony 702	Winter ant	37.43737, -122.16718	CTmin: 3-18-17 CTmax: 1-28-17	CTmin: 22.0 CTmax: 15.6	CTmin: 7 CTmax: 7
Arrillaga Gym Colony	Argentine ant	37.42931, -122.16360	CTmin: 3-11-17 CTmax: 3-4-17	CTmin: 22.8 CTmax: 20.1	CTmin: 5 CTmax: 6
Campus Drive Colony	Argentine ant	37.42254, -122.16214	CTmin: 3-11-17 CTmax: 3-4-17	CTmin: 23.7 CTmax: 20.4	CTmin: 5 CTmax: 8
Gilbert 3 Colony	Argentine ant	37.42957, -122.17084	CTmin: 3-11-17 CTmax: 3-4-17	CTmin: 23.9 CTmax: 16.7	CTmin: 5 CTmax: 8
Global Ecology Colony	Argentine ant	37.42885, -122.17902	CTmin: 3-16-17 CTmax: 3-16-17	CTmin: 22.0 CTmax: 22.0	CTmin: 8 CTmax: 7
Lantana Colony	Argentine ant	37.42566, -122.16108	CTmin: NA CTmax: 3-4-17	CTmin: NA CTmax: 24.4	CTmin: NA CTmax: 6
Serra Colony	Argentine ant	37.42423, -122.16614	CTmin: 3-16-17 CTmax: 3-16-17	CTmin: 22.6 CTmax: 22.6	CTmin: 6 CTmax: 8

observed ants continuously throughout the CTmax trial and noted the temperature at which individual workers lost coordination. We do not know whether the response to increased temperature that we observed reflected temperature directly or dehydration.

To measure CTmin, we placed individual workers into plastic 11 mL vials and sealed the top of the vials using cling film. We placed vials containing ants into a water bath at $\sim 20^\circ\text{C}$ and added ice to approximate a chilling gradient at $\sim -1^\circ\text{C}/2\text{ min}$. We observed the vials continuously and recorded the exact time at which ants entered chill comas (lost coordination and were not able to right themselves after being tipped over/falling over). We placed an iButton (Maxim Integrated, California, USA) in a randomly placed vial in our chilling array to record the temperature every second. We referenced the iButton temperature recording to determine the exact temperature at which ants entered chill comas. We could not achieve temperatures below 0°C using an ice water bath, so in cases when ants had not entered chill comas near 0°C , we transferred the chilling array to a chilled metal container to achieve sub-zero temperatures. For both CTmax and CTmin observations, we confirmed that ants had lost coordination by gently tapping the side of the vial.

We used linear mixed models to compare CTmax and CTmin temperatures between Argentine and winter ants. For both CTmax and CTmin, we ran a linear mixed model with main effects of species, temperature at which ants were collected in the field, and humidity at which ants were collected in the field, and a random effect of ant colony identity. We included temperature and humidity in the field at time of collection to see whether conditions in the field at time of collection influenced our results.

To quantify temperature-dependent walking speed in winter ants, we measured how long it took ants to walk 10 cm along natural foraging trails in the field at various temperatures. We observed walking speed at the same six winter ant colonies that were used for CTmin and CTmax measurements (described above), each of which had a consistent foraging trail running linearly and vertically up a nearby tree. Approximately 1.5m off the ground, we drew a 10 cm reference guide along the trail (but not on the trail to prevent covering or disturbing the trail). We returned to these sites at a variety of temperatures and measured the length of time it took ants to walk the 10 cm length. We recorded speeds for the first 10 ants that crossed the 10 cm length, including both ants going up and down the tree. We did not include observations of ants that doubled back before walking the 10 cm length or paused walking for $>5\text{ s}$. We thus only measured the velocity for ants that took a linear, vertical path along the trunk tree trunk in order to control for total distance traveled. We recorded air temperature, humidity, and surface temperature near the foraging trail at each observation before beginning walking speed data collection for a given colony. We collected data on winter ant walking speeds between 1/16/2017-1/28/2017, during air temperatures ranging from 3.6 to 14.6°C . We aimed to sample ant walking speed across the full range of ambient temperatures ants would experience in winter. We were not able to assess if winter ants forage at temperatures below 3.6°C or above 14.6°C .

In addition to our measurements, we used data previously collected by [Burford et al. \(2018\)](#) to quantify temperature-dependent walking speed in Argentine ants. These data were collected on the Stanford University campus during the same season, between 2/1/2016-3/14/2016. [Burford et al. \(2018\)](#) tested ant walking speeds using similar methods over three 24-h intervals, covering the daily range of ambient air temperatures ants would experience (between 6.3 and 24°C). [Burford et al. \(2018\)](#) did not assess whether Argentine ants continue foraging at temperatures below 6.3°C or above 24°C .

We collected data on temperatures in the greater Stanford area from the Norman Y. Mineta San Jose International Airport Weather Station ("San Jose, CA Weather History," 2022). We collected data on daily minimum temperatures from the month with the coldest minimum temperature of the year (January 2017), and on daily high temperatures from the month with the hottest maximum temperature of the year

(September 2017).

We averaged walking speed observations over single observation events. For winter ants, this included up to 10 ants going up or down the tree. For Argentine ants, this included up to 20 ants total: up to 10 going up the tree, and up to 10 going down the tree. We conducted simple linear regressions of speed by air temperature for each species to determine the slope of the best-fit line. For further analysis, we normalized ant speed and air temperature using a log transformation. We did this log transformation in order to address heteroscedasticity observed in the residuals when the model was initially run without a data transformation. We then created a comprehensive mixed effects model for $\log(\text{walking speed})$ with main effects of $\log(\text{air temperature})$ and species using colony as a random effect. To focus on temperature ranges where observed walking speeds overlap, we reran this same mixed effects model for only the range of temperatures at which walking speeds for both winter ants and Argentine ants were observed (6.4°C – 14.4°C). We then calculated the point at which these two linear regression lines intersected. We conducted a Q10 analysis using the temperatures and regression coefficients from this model. To calculate

Q10, we used the formula $Q_{10} = \left(\frac{R_2}{R_1}\right)^{\left(\frac{10}{T_2 - T_1}\right)}$ where T_1 and T_2 correspond to the maximum and minimum temperatures at which walking speed was observed for both species (6.4°C – 14.4°C) and R_1 and R_2 correspond to walking speeds from the regression model for those given temperatures. All statistical tests were performed in R (version 4.0.3) and RStudio (version 1.3.1093) using packages tidyverse, FSA, car, and lme4. Model results from untransformed data are presented in the Supplement.

3. Results

In both our data on winter ants, and those of [Burford et al. \(2018\)](#) on Argentine ants, air temperature was strongly correlated with tree surface temperature (Pearson correlation coefficient = 0.81) and humidity (Pearson correlation coefficient = -0.72), so our analysis included air temperature but not tree surface temperature.

Winter ants had a significantly lower CTmin than Argentine ants, accounting for colony-level differences as a random effect ($t = -5.32$, $p = 1.04 \times 10^{-7}$; [Fig. 1](#)). Winter ants entered chill comas at $0.06 \pm 0.93^\circ\text{C}$ (mean CTmin \pm SD), and Argentine ants entered chill comas at $2.4 \pm 1.12^\circ\text{C}$. Temperature and humidity at the time of collection did not influence CTmin ($t = -1.75$, $p = 0.081$ temperature; and $t = -1.55$, $p = 0.12$ humidity).

Winter ants and Argentine ants had similar CTmax values. At high temperatures, winter ants lost coordination at $42.4 \pm 0.78^\circ\text{C}$ (mean CTmax \pm SD), and Argentine ants lost coordination at $42.8 \pm 2.38^\circ\text{C}$. This difference in CTmax values was not statistically significant, accounting for colony-level differences as a random effect ($t = -1.13$, $p = 0.26$; [Fig. 1](#)). For each species, temperature and humidity at the time of collection did not influence CTmax ($t = -0.52$, $p = 0.60$ temperature; $t = -1.25$, $p = 0.21$ humidity).

Both winter ants and Argentine ants increased their walking speed with increasing temperature. Temperature was strongly positively correlated with ant walking speed ($t = 18.41$, $p < 10^{-10}$). The temperature by ant species effect was also strongly significant ($t = -3.74$, $p < 0.001$). The best-fit regression line for Argentine ants had a slope of $0.077\text{ cm/s}/^\circ\text{C}$, while the best-fit regression line for winter ants was less than half as steep, with a slope of $0.033\text{ cm/s}/^\circ\text{C}$ ([Fig. 2](#)).

For the model using only data from the overlapping temperature range, temperature was strongly positively correlated with ant walking speed ($t = 12.37$, $p < 10^{-8}$, [Supplemental Fig. 1](#)). The temperature by ant species effect was also significant ($t = -2.44$, $p = 0.015$, [Supplemental Fig. 1](#)). These results were consistent with the that included the full range of temperatures. The linear regression lines for both species intersected at 7.14°C ; below 7.14°C winter ants walked faster than Argentine ants. Argentine ant walking speed had a Q10 value of 4.07

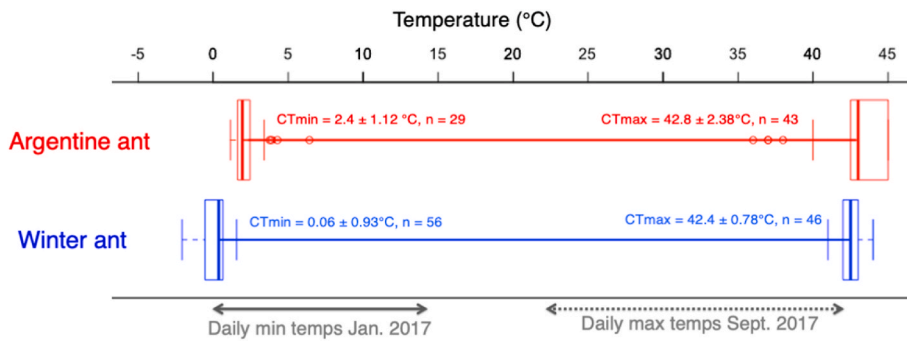


Fig. 1. Critical thermal maxima and minima for Argentine ants (red) and winter ants (blue). Labels display critical thermal maxima and minima \pm standard deviation of the mean and sample size. Arrows show daily minimum temperatures for Jan. 2017 (the month with the coldest minimum temperature, 0–14 °C, solid gray) and daily maximum temperatures for Sept. 2017 (the month with the hottest maximum temperature, 22–42 °C, dashed gray). Circles represent outliers. Boxplots show CTmax and CTmin data collected, while bolded, solid horizontal lines represent ranges of thermal tolerance based on these critical limits for each species.

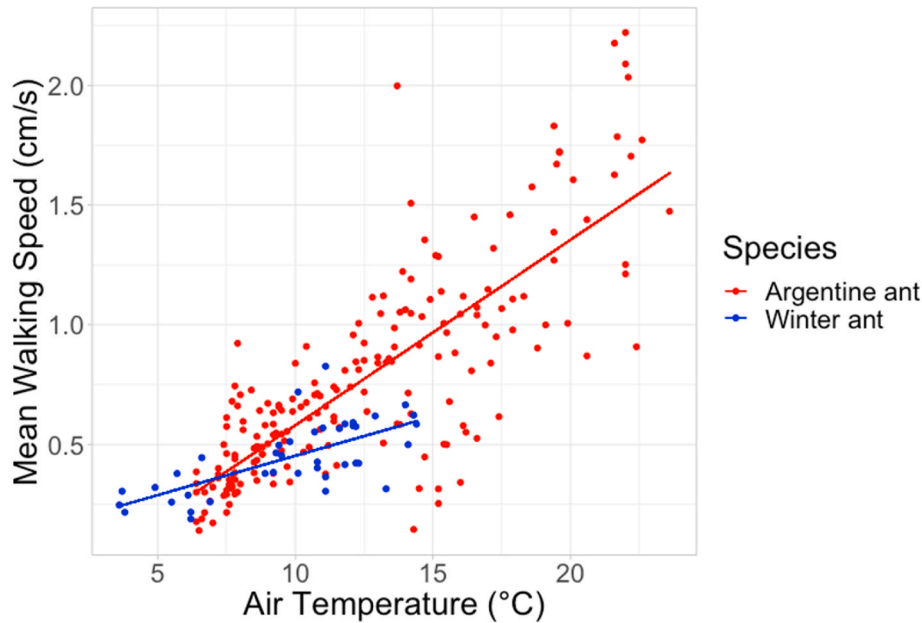


Fig. 2. Temperature dependent walking speed for Argentine ants (red) and winter ants (blue). Lines show linear regressions. Each point represents averaged walking speeds over a single colony observation. Data on Argentine ant walking speeds were collected by [Burford et al. \(2018\)](#).

and winter ant walking speed had a Q10 value of 2.05.

4. Discussion

Winter ants had a significantly lower CTmin than Argentine ants, while both species had similar values for CTmax. Both species walked faster with increasing temperature, but Argentine ants had a higher rate of change in speed per degree change in temperature than winter ants.

At temperatures that ants experience in their natural environment, 0–2.5 °C, winter ants may be active while Argentine ants are in chill comas, allowing winter ants to forage on cold winter days when Argentine ants cannot. Winter ants had a CTmax that was equivalent to that of Argentine ants, suggesting that winter ants are similarly physiologically capable of summer activity. Instead, reduced summer activity could help winter ants avoid competition with Argentine ants and other native ants in natural systems, e.g. *Formica moki* and *Camponotus semitestaceus* are both active in summer months ([MacArthur-Waltz et al., 2021](#)). Although seasonal activity patterns could be driven by caring for existing brood, evidence suggests that winter ants do not have brood present in the nest in the winter ([Talbot, 1943](#)). These results suggest that winter ants have a broader thermal niche than Argentine ants, lending support to the climate variability hypothesis.

The winter ant's walking speeds were significantly less temperature-dependent than those of the Argentine ant, enabling the winter ant to

remain active at comparatively lower temperatures. At temperatures below \sim 7 °C, winter ants can move faster than Argentine ants, potentially allowing them to forage more quickly in cold weather. Temperature-dependent walking speed may represent a more biologically meaningful measurement of thermal performance than CTmin/max because measurements of temperature-dependent walking speed reflect actual responses to temperature in the field. These ants often forage for food far from their nest by walking up tree trunks to reach the canopy, so their walking speed likely influences the time it takes to complete a foraging trip.

High temperatures can allow ectotherms to generate and increase their use of ATP and can increase their metabolic rates ([Gillooly et al., 2001](#); [Clarke and Fraser, 2004](#)). Ants walking at higher temperatures may thus experience increased metabolic activity. Argentine and winter ants differed in their Q10 for walking speed, suggesting that these two ant species may have different metabolic responses to temperature. Future research could explicitly model Argentine and winter ant walking speed and foraging trail length to investigate how temperature influences ant foraging outcomes and energetics. While our results are consistent with past work that suggests ant walking speed is highly temperature-dependent ([Hurlbert et al., 2008](#)), future work should aim to further disentangle the relative influence of ambient temperature from temporal variation in thermal acclimatization and resource availability on walking speed.

Because winter ant walking speeds do not increase as rapidly with temperature as those of Argentine ants, winter ants may not be able to forage as quickly at high temperatures. During primarily warmer months (May–November), Argentine ants located bait food sources faster than native ants and were likely to retain control of those food sources once they were found (Human and Gordon, 1996). In addition to fast walking speed, large colony size and colony density may increase the number of foraging trips completed by Argentine ants in a given area. Moreover, Argentine ants can displace native ant species from food resources through aggressive behavior (Human and Gordon, 1996). Temperature could further influence the frequency and intensity of interspecific aggression in Argentine ants. These findings suggest that winter ants may be at a disadvantage when foraging in warmer months where Argentine ants are present.

The observed differences in thermal niche breadth suggest that climate change may alter the coexistence dynamics between Argentine and winter ants. Winter ants can physiologically tolerate a range of colder temperatures than Argentine ants, suggesting that winter ants may lose their ability to coexist if temperatures increase out of this range, or that they may be limited to cooler microclimates that serve as thermal refugia.

Our result that winter ants have a low CT_{min} is consistent with previous field studies, showing that winter ants can remain active at temperatures slightly below 0 °C (Fellers, 1989). Most ectotherms that lack specialized cold tolerance adaptations are inactive below 0 °C (Sunday et al., 2011). Winter ants show differential gene expression in response to varying temperatures, suggesting that such variation in gene expression could be relevant for adaptation to climate change (Tonione et al., 2020a). Further work is needed to examine how relationships between ant walking speed and temperature are linked mechanistically to biochemical pathways and predictions.

In addition to foraging efficiency, other factors may contribute to coexistence between Argentine and winter ants, including a highly lethal defensive secretion winter ants use against Argentine ants (Sorrells et al., 2011). Argentine ants often retreat into aggregations during the winter, which may provide more foraging opportunities for winter ants. However, Argentine ants have been observed to forage heavily from winter aggregations at the site studied here (Burford et al., 2018). Finally, Argentine ants rely on the availability of consistent water sources; the lack of available water can limit their distribution during droughts (Holway et al., 2002; Menke and Holway, 2006). Winter ants expanded their spatial distribution relative to Argentine ants during drought years (Couper et al., 2021), suggesting that access to water may influence the interaction between winter ants and Argentine ants.

Invasive species often experience selection in their introduced range that differs from selection in their native range (Han and Dong, 2020; Perkins et al., 2013). Thermal variability can play a role in driving rapid adaptation in invasive species (Han and Dong, 2020), underscoring the need to investigate whether Argentine ants' exposure to novel climates has resulted in local adaptation in their invasive range. Argentine ants have primarily invaded Mediterranean ecosystems, suggesting that broader temperature ranges may limit their invasion into more temperate climates.

For winter ants, thermal tolerance has been previously documented across multiple populations in California (Tonione et al., 2020b). Higher elevation populations of winter ants display greater cold tolerance and greater thermal plasticity (Tonione et al., 2020b), and further work is needed to investigate this pattern. We were able to measure thermal niche only in a single population. Future research is needed to investigate whether winter and Argentine ants coexist in areas that are warm enough for Argentine ants to remain active all winter across a broader range of ant populations. Native ant species that have been displaced by Argentine ants may have more overlap with Argentine ants in their thermal breadth than winter ants. Future work could measure critical thermal limits and temperature-dependent walking speeds for these native species.

5. Conclusion

In conclusion, our data demonstrate that winter ants had a significantly lower CT_{min} than Argentine ants and walked faster than Argentine ants at colder temperatures, but were able to tolerate similarly warm temperatures to Argentine ants. The results raise intriguing questions about how differences in thermal breadth influence the ability of winter ants to coexist with the invasive Argentine ant, and how these dynamics will be altered by ongoing climate change.

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CRediT authorship statement

Conceptualization; RAN, DMW, DMG Data curation; RAN, DMW Formal analysis; RAN, DMW Investigation; RAN, DMW Methodology; RAN, DMW, DMG Project administration; RAN, DMW, DMG Resources; RAN, DMW, DMG Software; RAN, DMW, DMG Supervision; DMG Validation; RAN, DMW, DMG Visualization; RAN, DMW, DMG Roles/Writing - original draft; RAN, DMW, DMG Writing - review & editing. RAN, DMW, DMG.

Declaration of competing interest

The authors have no competing interests to declare.

Data availability

Data are accessible at <https://doi.org/10.25740/xd864rp1501>. Full citation for data repository: Nelson, R., MacArthur-Waltz, D., Gordon, D., 2022. Critical thermal limits and temperature-dependent walking speed may mediate coexistence between the native winter ant (*Pre-nolepis imparis*) and the invasive Argentine ant (*Linepithema humile*). Stanford Digital Repository Available at <https://purl.stanford.edu/xd864rp1501>.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jtherbio.2022.103392>.

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