Northward Expansion of the Invasive *Linepithema humile* (Hymenoptera: Formicidae) in the Eastern United States is Constrained by Winter Soil Temperatures

R.J. BRIGHTWELL, P.E. LABADIE, AND J. SILVERMAN[1]

Department of Entomology, North Carolina State University, Raleigh NC 27695-7613

Environ. Entomol. 39(5): 1659–1665 (2010); DOI: 10.1603/EN09345

ABSTRACT The invasive Argentine ant, *Linepithema humile* (Mayr) (Hymenoptera: Formicidae) has been evident in the North Carolina Piedmont, United States for 90 yr but has failed to spread further north. We investigated the mechanisms preventing this expansion. The Argentine ant ceases foraging at temperatures below 5°C and we hypothesized that winter soil temperatures at higher latitudes restricted foraging long enough to cause colony starvation. We tested if the Argentine ant could successfully feed at temperatures below 5°C and found that colonies would starve. We subjected Argentine ant nests to a range of sub- and above-freezing temperatures and measured worker mortality at various time intervals. We found that Argentine ant colonies will collapse after 8.5 d at 5°C. Argentine ants can escape ambient cold temperatures by moving nests into the soil column. We tested how deeply into the soil Argentine ant queens and workers need to move to survive winter in North Carolina. Soil temperatures in the North Carolina Piedmont do not fall below 5°C for longer than nine consecutive days; therefore, Argentine ant colonies need only to retreat a few centimeters into the soil column to escape unsuitable temperatures. Winter soil temperature data from four climate stations situated from latitudes 35°, the current Eastern United States latitudinal limit for Argentine ant population expansion, to 39° were searched for periods where soil temperatures would have led to colony extirpation. North of their current distributions, extended periods of soil temperatures below 5°C regularly occur, preventing Argentine ant colonies from persisting.

KEY WORDS abiotic interactions, environmental limitation, invasive species, range limitation, low temperature

A primary goal of invasion biology is to predict the potential distribution of an introduced species. Factors contributing to an organism's successful establishment have generally been divided into either biotic interactions (Simberloff and Von Holle 1999, Stachowicz et al. 1999, Torchin et al. 2003) or abiotic interactions (Moyle and Light 1996, Blackburn and Duncan 2001, Gabriel et al. 2001, McGeoch et al. 2006). For invasive ants, invasion success is often influenced more by environmental and climatic conditions than biotic interactions (Holway et al. 2002b, Krushelnycky et al. 2005, Menke et al. 2007). Meta-analysis and modeling have identified mean winter temperatures as an important climatic limiter on the successful establishment of invasive ants (Korzukhin et al. 2001, Morrison et al. 2004, Lester 2005, Hartley et al. 2006). Global warming has been implicated in a number of species, including arthropods, increasing their range into higher latitudes (Parmesan and Yohe 2003). This suggests that invasive ant species may be set to increase their introduced range into higher latitudes as world temperatures warm. In this study, we describe how winter soil temperatures prevent an invasive ant from expanding its range along the eastern seaboard of the United States.

The Argentine ant, *Linepithema humile* (Mayr) (Hymenoptera: Formicidae), is a significant invasive ant species capable of disrupting both natural and managed environments (Holway et al. 2002b, Silverman and Brightwell 2008). This ant is now widely distributed around the world (Suarez et al. 2001). *L. humile* prefers Mediterranean climates but can be found in some subtropical and warm temperate regions of the world (Roura-Pascual et al. 2006). The potential range of *L. humile* is thought to be severely restricted by cool temperatures (Hartley and Lester 2003, Buczkowski et al. 2004, Krushelnycky et al. 2005, Hartley et al. 2010). *L. humile* is most likely to be evident in areas where mid-winter mean daily temperatures range between 7–14°C (Hartley et al. 2006). Prolonged exposure to subfreezing temperatures are lethal to *L. humile* (Herbert 1932, Jumbam et al. 2008). However, *L. humile* is known to escape adverse winter conditions by nesting in the top few centimeters of soil (Newell and Barber 1913, Heller and Gordon 2006).

---

[1] J. Silverman, e-mail: jules_silverman@ncsu.edu.

Established populations of *L. humile* have existed in the North Carolina Piedmont on the east coast of the United States since 1919 (Smith 1919). This has been the northern limit for *L. humile* ever since (Smith 1936, Suarez et al. 2001). Across the North Carolina Piedmont, mid-winter mean daily temperatures range from 1.6 to 4.4°C (State Climate Office [SCO] 2009), lessening the risk of nest extirpation from freezing. However, this range is well below the mean mid-winter temperature envelope proposed by Hartley et al. (2006). *L. humile* generally ceases active foraging when ambient temperatures fall below the minimum foraging temperature of 5°C (Markin 1970, Witt and Giliomee 1999, Krushelnycky et al. 2005). During North Carolina winters, *L. humile* is abundant around loblolly pine, *Pinus taeda* (Pinales: Pinaceae). Even when ambient temperatures have dropped below 5°C *L. humile* can be observed trailing on the sun-warmed bark, apparently feeding on honeydew (R.J. Brightwell, personal observation). *P. taeda* can be found as far north as southern New Jersey (Baker and Langdon 1990). The range of *Toumeyella virginiana* (Hemiptera: Coccidae), the apparent source of honeydew, extends north to Maryland (Williams and Kosztarab 1972). This suggests that a lack of a winter food resource is not the limiting factor in the northward expansion of *L. humile.*

We hypothesized that winter soil temperatures beyond the current range of *L. humile* are consistently too cold to permit enough foraging to prevent colony starvation. In laboratory experiments we correlated time to worker extirpation with temperature and developed a linear model for colony extirpation of *L. humile.* We then calibrated how deeply into the soil *L. humile* will migrate to escape winter conditions and collected January soil temperature data from four climate stations located from North Carolina to Maryland. From this soil temperature data we determined if *L. humile* nests could consistently survive winter north of its current range. If winter soil temperature does currently restrict the northward spread of *L. humile,* one can expect this invasive ant to extend its range as global temperatures warm.

Materials and Methods

***L. humile* Cold Temperature Acclimation.** Because we were using laboratory colonies of *L. humile* to investigate cold temperature survival, we first tested for evidence of cold temperature acclimation in field colonies of *L. humile* collected from a commercial park in Raleigh, NC. Laboratory nests were created from laboratory colonies collected the previous summer from the same commercial park. These laboratory colonies were kept at 26°C and 50% RH and were supplied ad libitum with 25% sucrose water and fed artificial diet (Bhatkar and Whitcomb 1970) and freshly killed German cockroaches, *Blattella germanica* (Blattodea: Blattellidae), weekly. Field colonies were collected on the day the experiment was started in March from the same commercial park. Forty-eight experimental nests were created, 24 nests from the laboratory colony and 24 nests from the freshly collected field colony. Each experimental nest consisting of two queens and 100 workers were created and housed in 591 ml plastic containers (S.C. Johnson and Son Inc., Racine WI) with fine mesh panels glued into the lid and bottom of the container to allow airflow. Each replicate contained a moistened plaster nest measuring 80 mm in diameter and was supplied with water, 25% sucrose water and 0.5 ml artificial diet. These liquids were contained within a 6 × 50 mm disposable culture tube with a cotton wick. All experimental nests were subjected to constant conditions of −2°C and 50% RH in an incubator. Worker mortality was recorded after 24, 48, and 72 h. eight field and eight laboratory nests were removed at each time period that the surviving workers were counted. These nests were then discarded. There was very little queen mortality during this experiment and, therefore, queen mortality was not analyzed. Worker survival was analyzed by PROC GLM Tukey's nonparametric test (SAS Institute 2004).

Cold Temperature Survival of *L. humile.* The effects of various cold temperatures versus survival time on *L. humile* and the odorous house ant, *Tapinoma sessile* (Say) (Hymenoptera: Formicidae), were tested. We used *T. sessile* as a control to ensure our protocols were suitable. *T. sessile* is distributed from Mexico to Canada and is known to survive extremely low temperatures (Smith 1928, Buczkowski and Bennett 2008), therefore, *T. sessile* survival would demonstrate that any observed *L. humile* mortality was caused by cold temperature rather than ant containment. *L. humile* nests were created from the same laboratory colonies described above. *T. sessile* colonies were created from laboratory colonies collected from Rocky Mount, NC, and were housed as described above. Nests from laboratory colonies, consisting of one queen and 100 workers, were created for both *L. humile* and *T. sessile* and housed and fed as described above. The nests were placed for various periods in a darkened incubator. The incubator was maintained at one of four temperature regimes, −4, −2, 0, and 4°C at 50% RH. Four *L. humile* and four *T. sessile* nests were retrieved after 0.5, 1, 3, 4, or 6 d, which was predetermined by the temperature regime. The retrieved nests were held at 26°C for 1 h to thaw and surviving *L. humile* and *T. sessile* workers were then counted. Data were analyzed with PROC GLM with temperature and time as independent variables and worker survival as the dependent variable (SAS Institute 2004). A linear regression model for colony extirpation was then calculated from the linear regressions of *L. humile* survival at each temperature.

Survival With and Without Food at Low Temperatures. We tested if *L. humile* could successfully feed at 4°C to determine if temperatures below the minimum foraging temperature of 5°C, but above freezing, would prevent feeding on nearby food resourses and lead to starvation. We chose 4°C to ensure any fluctuations in incubator temperature did not exceed 5°C. *Linepithema humile* nests were created from laboratory colonies collected from the field and consisted of one queen and 100 workers and a few brood. The experimental nests were housed as described above. The experimental nests were subjected to differing temperature and food regimes. Nests were allocated to a constant temperature of either 4 or 26°C with relative humidity held at 50%. For each temperature, five nests were assigned to one of three food regimes consisting of water, water plus 25% sucrose-water, or water, 25% sucrose-water and canned tuna. Water and sucrose-water were presented in 6 × 50 mm disposable culture tubes (FisherScientific, Pittsburgh, PA) with a cotton wool wick. Approximately 1 g of tuna was presented in a 40 × 40 × 8 mm weighing dish. Weekly counts of surviving workers were undertaken for 3 wk. After surviving workers were counted, dead ants were removed and all water tubes, sucrose-water tubes, and tuna were replaced, ensuring that nests did not run out of any allocated food resource. Treatment effects on ant mortality were analyzed with PROC GLM repeated measures (SAS Institute 2004).

Winter Soil Temperatures and Nesting Depth. We investigated whether *L. humile* find refuge from low (subzero) winter temperatures in Raleigh, NC, by moving down into the soil and, if so, were their nests randomly distributed throughout the soil column or aggregated at certain strata. Columns consisting of five 50 mm sections of PVC pipe (100 mm diameter) were packed with degraded pine mulch and sealed by nylon mesh allowing both vertical and horizontal movement of *L. humile* workers and queens within the column. Each section was supplied with water and sucrose water and freshly killed *B. germanica* and artificial diet, as described above. These sections were stacked vertically within a closely fitted outer PVC column (250 mm length) with the column capped at both ends to prevent escape. The columns were buried in the soil with the top of the column flush with the ground.

On the day the columns were buried in the soil, *L. humile* workers and queens were collected at the field site. One thousand workers, two queens, and an undetermined quantity of brood were introduced to the top section of each column. Two trials were conducted, the first at the end of January and the second at the end of February, each running for 7 d. The *L. humile* fragments were placed into the column at 1600 h on days when afternoon ambient temperature was warm enough to allow the ants to move within the column. The columns were removed at 0900 h on the seventh day when ambient temperatures were still cool and the ants could be captured in their preferred sections. Five replicates were performed in each trial. The first trial lost one replicate when the top of one column was destroyed by heavy machinery allowing the possible entry of local *L. humile* workers and queens. Temperature data loggers (Onset Computer Corporation, Bourne, MA) were placed on the soil surface and 50, 100, 150, 200, and 250 mm into the soil column for both the January and February trials. Data were analyzed with PROC FREQ Pearson's χ^2 test with position of the ants within the vertical column and month of trial as our observed variables (SAS Institute 2004).

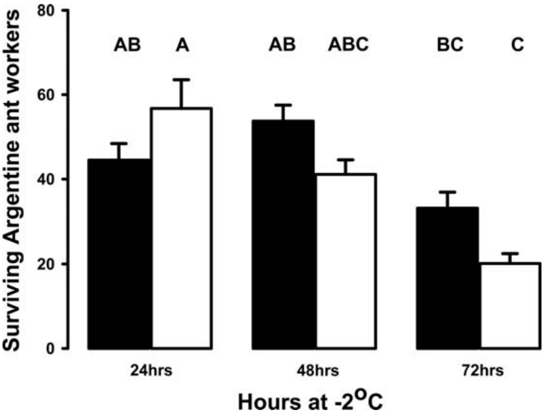

Fig. 1. Mean survival (±SE) of field collected and laboratory maintained Argentine ant nests to sub-freezing temperatures. Argentine ant worker survival was assessed after 24, 48, and 72 h at −2°C. Black bars represent mean Argentine ant nests assembled from field colonies collected directly from the field. Unfilled bars represent mean Argentine ant nests assembled from stock laboratory colonies originally collected from the same location. Nests consisted of two queens and 100 workers. $\alpha = 0.05$.

Northward Expansion Potential of *L. humile*. January soil temperature data from 5 yr (2005–2009) was collected from four Soil Climate Analysis Network stations (SCAN 2009) at Tidewater, NC; Reynolds Farm and North Piedmont, VA; and Powder Mill, MD, with latitudes ranging from 35°52′ to 39°01′. We chose January because it is usually the coldest month of the year surveyed. Temperature data from soil depths of 50, 100, 200, and 500 mm were used in this analysis. *L. humile* is known to cease foraging at 5°C therefore we determined, from our temperature-time nest extirpation curve, the length of time below 5°C necessary to extirpate an *L. humile* colony. January soil temperature data from the four climate stations was searched for periods where soil temperature remained below 5°C long enough to extirpate a colony.

Results

***L. humile* Cold Temperature Acclimation.** There was no evidence for cold weather acclimation in *L. humile* with worker survival between the laboratory and field colonies being the same over any of the individual time ranges (Fig. 1). As expected, worker survival, for both field and laboratory colonies, decreased as their exposure to sub-freezing temperatures increased.

Cold Temperature Survival of *L. humile*. *T. sessile* showed little appreciable mortality across all temperatures indicating that our methodology was valid. When laboratory *L. humile* nests were subjected to −4, −2, 0 or 4°C their survival was lower than *T. sessile* ($F = 2.83$; df = 1, 4; $P = 0.0296$). *L. humile* nest extirpation occurred after a few days at these temperatures (Fig. 2). The estimated time to nest extirpation from *L. humile* worker mortality for each of the

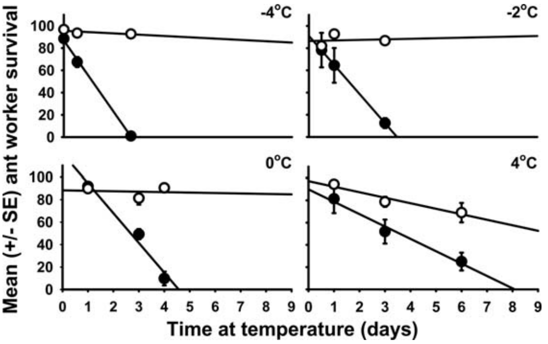

Fig. 2. Mean survival (±SE) of Argentine ant and odorous house ant workers subjected to a variety of cold temperatures. ● Argentine ants. ○ odorous house ants. Nests consisted of one queen and 100 workers for both species. Temperature was kept constant at the indicated temperature with a constant RH of 50%.

four temperatures was calculated (Table 1) with time to nest extirpation showing a strong linear correlation with temperature (Fig. 3).

Survival With and Without Food at Low Temperatures. *L. humile* nests subjected to 26°C and provided with sucrose water or sucrose water and tuna had high worker survival through 3 wk (Fig. 4; Table 2). The *L. humile* nests subjected to 4°C had poor survival regardless of the food regime offered and were extirpated by the third week (Fig. 4; Table 2). Interestingly, those nests subjected to water only but kept at 26°C showed similar mortality to those nests kept at 4°C, indicating that mortality was consistent with starvation rather than cold.

Winter Soil Temperatures and Nesting Depth. When *L. humile* colony fragments were free to move within the soil column they consistently chose to remain close to the soil surface (χ^2 = 68.45; df 4; $P <$ 0.0001; Fig. 5). *L. humile* colony fragments were higher in the soil column in February than in January (χ^2 = 4.92; df 1; P = 0.0264; Fig. 5). *L. humile* colonies could move merely a few centimeters below the soil surface to escape freezing temperatures. Soil surface temperatures for the January trials fluctuated widely compared with further down into the soil column with temperatures ranging from −2.4 to 25.5°C with a mean temperature of 7.4°C. For the February trial the soil surface temperature ranged from −5.3 to 17.9°C with a mean of 6.8°C. In contrast, the minimum and maximum soil temperatures, to a depth of 200 mm, ranged from 4.5 to 10.2°C in January and 6.6 to 17.9°C in February with mean temperatures of 6.8 and 8.1°C, respectively.

Table 1. Linear regression models of Argentine ant nest survival at four temperatures with the estimate of time to zero worker survival

Temperature (°C)	Regression equation	r^2	Time to zero worker survival (days)
−4	y = 104.08–34.50x	0.9982	3.0
−2	y = 91.07–26.21x	0.9999	3.4
0	y = 120.82–26.46x	0.9717	4.5
4	y = 89.89–11.11x	0.9803	8.0

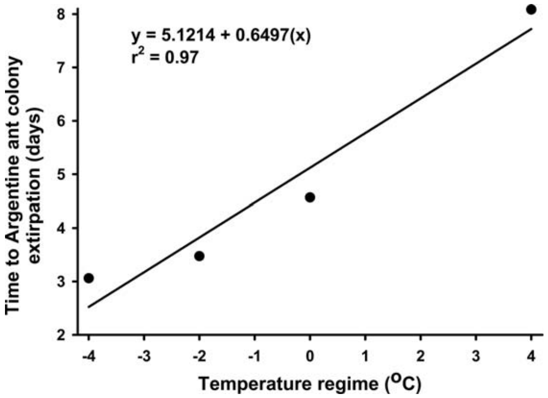

Fig. 3. Linear model of time to Argentine ant colony extirpation as a function of constant temperature. Linear regression for time to zero worker survival was calculated for four temperatures (Table 1). The estimated times to colony extirpation were then used to calculate an ant colony extirpation model.

Northward Expansion Potential of *L. humile*. Our model of colony extirpation indicated that there would be 100% worker mortality after 8.5 d at a constant 5°C. We rounded this time up and considered periods of 9 d at temperatures below 5°C as lethal to *L. humile* colonies. January soil temperature data for each climate station were searched for such periods. *L. humile* would have survived all 5 yr in Tidewater, NC, at any soil depth analyzed. For the three northern climate stations, prolonged cold

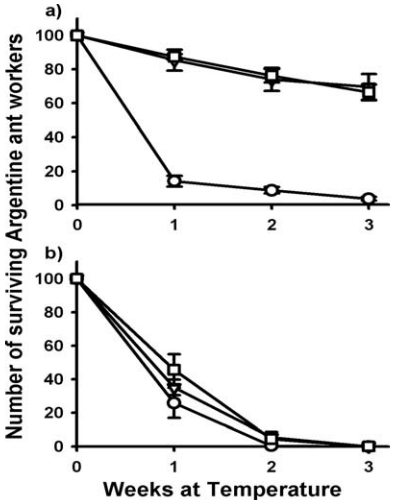

Fig. 4. Mean (±SE) number of surviving Argentine ant workers through 3 wk under differing food regimes at a constant temperature of (a) 26°C and (b) 4°C. All nests consisted of one queen, 100 workers, and a few brood. ○ Nests were subjected to a food regime of water only. ▽ Nests were supplied with water and sucrose-water. □ Nests were supplied with water, sucrose-water, and ≈1 g of tuna.

Table 2. Repeated measures analysis of Argentine ant nest survival at cold temp (4°C) compared with mid-optimal foraging temp (26°C) when subjected to three food regimes; water only; water and sucrose-water; and water, sucrose-water, and tuna

Variable	df	*F* value	*P* value
Food regime	2	62.257	<0.0001
Temp regime	1	172.359	<0.0001
Temp × food interaction	2	42.741	<0.0001
Error	24		

soil temperatures would have lead to *L. humile* colony extirpation at least once during the 5 yr surveyed regardless of the soil depth. This indicates that *L. humile* could not successfully establish at these northern latitudes (Table 3).

Discussion

Field colonies of *L. humile* did not appear to acclimate to low temperatures indicating that laboratory colonies would accurately reflect field colony responses. Unlike the cold-tolerant *T. sessile, L. humile* workers died within days when subjected to low temperatures. We found a strong linear correlation between temperature and time to worker extirpation. *L. humile* apparently starved when temperatures remained consistently below the minimum foraging temperature of 5°C even though food was available. In Raleigh, NC, *L. humile* found a nesting refuge within the top 200 mm of soil with sub-surface temperatures consistently remaining above 5°C during the winter months. January soil temperatures north of current North Carolinian infestations remained below 5°C long enough to prevent successful establishment.

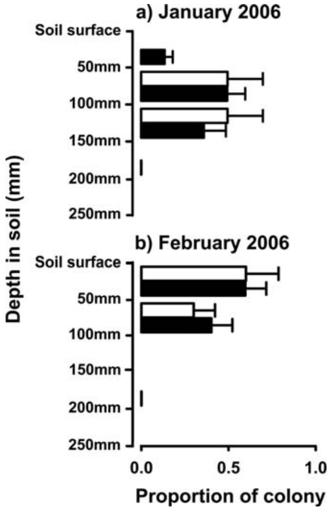

Fig. 5. Mean stratification of workers and queens (±SE) in the soil column during January and February in North Carolina. Black bars represent mean Argentine ant workers. Unfilled bars represent mean Argentine queens. Nests consisted of two queens and 1,000 workers.

Table 3. Total no. of Januarys in a 5-yr period (2005–2009) when an Argentine ant colony would fail because of restricted foraging

Location	Latitude[a]	Soil depth (mm)			
		50	100	200	500
Powder Mill, MD	39°01′	3	3	3	2
Northern Piedmont, VA	38°14′	3	3	3	1
Reynolds Farm, VA	36°39′	3	2	3	1
Tidewater, NC	35°52′	0	0	0	0

[a] Length of 1 degree of latitude at 35° North ≈111 km.

Colony extirpation is assumed when there was more than nine consecutive days with temperatures remaining below 5°C (calculated from colony extirpation formula Fig. 3). Soil temperatures at the displayed depths were obtained from Soil Climate Analysis Network station recordings. Soil temp readings were taken hourly.

Jumbam et al. (2008) found weak support for short-term acclimation of *L. humile* to sub-zero temperatures over 4 hr. We observed no acclimation effects when we subjected our field and laboratory colonies to −2°C for 24–72 h. It appears that any cold temperature acclimation effects are measured in hours rather than days. Even when subjected to nonfreezing temperatures *L. humile* queens and workers die fairly quickly. Low winter temperature has previously helped explain restrictions to *L. humile* spread (Krushelnycky et al. 2005, Menke et al. 2007, Hartley et al. 2010). When we held temperatures below 5°C, workers and queens were trapped within the nest and unable to feed, eventually leading to colony starvation. Jumbam et al. (2008) found that *L. humile* was capable of some activity at temperatures approaching 0°C, somewhat below the minimum foraging threshold of 5°C ambient temperature deduced by Markin (1970). However, Jumbam et al. (2008) suggested that active load carrying may become impracticable as transport costs increase with lowering temperatures. *L. humile* queens have low body fat content and the available fat cannot sustain them for extended periods (Keller and Passera 1988). Additionally, *L. humile* queens cannot survive without workers (Hee et al. 2000) so worker survival is critical to colony survival. Soil temperatures that remain below the minimum foraging threshold for longer than 9 d will result in the extirpation of a colony's workers, which, in turn, will result in the death of the queens and the failure of the colony.

L. humile are most likely to be found in areas with mid-winter mean daily temperatures ranging between 7 and 14°C, a temperature range that would ensure regular winter foraging opportunity (Hartley et al. 2006). Heller and Gordon (2006) noted that *L. humile* would choose warmer nest sites in winter and cooler nest sites in summer to help regulate colony temperature. In more temperate regions cool summer temperatures may limit *L. humile* spread with prolonged developmental rates jeopardizing long-term successful establishment (Hartley and Lester 2003, Abril et al. 2009). Previous studies investigating the effects of soil temperature on *L. humile* have concentrated on the interactions between soil surface temperature and worker foraging (Human et al. 1998, Witt and Giliomee 1999, Holway et al. 2002a). Hartley et al. (2010) examined the effects of subsurface soil temperatures on worker development and colony establishment. In this study we demonstrate that winter subsurface soil temperature may be critical for continued survival of *L. humile* colonies by restricting worker movement from the nest, leading to colony starvation.

L. humile find refuge from cold winter temperatures in the North Carolina Piedmont by retreating underground. This behavior has been noted previously with nests being found to a depth of 350 mm (Newell and Barber 1913). We found *L. humile* workers and queens aggregated within the top 150 mm of soil during winter months in Raleigh, NC. Though sub-soil temperatures were lower and *L. humile* nests deeper in the soil column in January than in February, we are hesitant to draw conclusions on the effect of month since our study was conducted within a single calendar year. Winter soil temperatures remained warm enough in North Carolina to allow workers to leave the nest, providing adequate winter foraging opportunities for *L. humile* colonies to survive over the 5-yr period surveyed. As previously mentioned, *L. humile* have been observed foraging on sun-warmed *P. taeda* even when ambient temperatures are below 5°C. This can only occur if the soil is warm enough to allow *L. humile* workers to move out of the nest. Conversely, at higher latitudes winter sees prolonged periods when soil temperatures would restrict workers from leaving the nest, restricting winter foraging opportunities and preventing long-term successful establishment of *L. humile.* Winter soil temperatures appear to be a major limiter to the potential spread of *L. humile* along the eastern seaboard of the United States.

Environmental conditions appear to be extremely important in limiting the spread of *L. humile.* These abiotic limiters include soil moisture (Holway et al. 2002a), humidity (Walters and Mackay 2003), rainfall (Krushelnycky et al. 2005, Heller et al. 2008), and high temperatures (Holway et al. 2002a, Walters and Mackay 2004). Hartley et al. (2010) demonstrated that low annual soil temperatures may restrict *L. humile* establishment and spread by limiting successful worker development. Soil need not freeze to limit *L. humile* survival; soil temperatures cool enough to restrict workers from moving out of their nests can precipitate worker and queen extirpation and result in colony failure. Our model shows that *L. humile* colony extirpation will result when soil temperatures remain at or below 5°C for 9 d, conditions that occurred on a regular basis at latitudes above North Carolina. We suggest that the northern spread of *L. humile* on the east coast of the United States has been halted for ≈90 yr as winter soil temperatures north of North Carolina are too cold, for too long, to support establishment and ongoing survival. If winter soil temperatures rise along the United States eastern seaboard we predict a northward spread of this invasive ant.

Acknowledgments

We thank S. Menke, E.K. Spicer, and two anonymous reviewers for their helpful comments on the manuscript. We also thank A. Carper for his technical help and C. Arellano for statistical advice. This work was supported by the Blanton J. Whitmire Endowment at North Carolina State University.

References Cited

Abril, S., N. Roura-Pascual, J. Oliveras, and C. Gomez. 2009. Assessing the distribution of the Argentine ant using physiological data. Acta Oecol. 35: 739–745.

Baker, J. B., and O. G. Langdon. 1990. Loblolly Pine. *In* R. M. Burns and B. H. Honkala [eds.], Silvics of North America. United States Department of Agriculture Forest Service, Washington, DC.

Bhatkar, A. P., and W. H. Whitcomb. 1970. Artificial diet for rearing various species of ants. Fla. Entomol. 53: 229–232.

Blackburn, T. M., and R. P. Duncan. 2001. Determinants of establishment success in introduced birds. Nature 414: 195–197.

Buczkowski, G., and G. Bennett. 2008. Seasonal polydomy in a polygynous supercolony of the odorous house ant, *Tapinoma sessile.* Ecol. Entomol. 33: 780–788.

Buczkowski, G., E. L. Vargo, and J. Silverman. 2004. The diminutive supercolony: the Argentine ants of the southeastern United States. Mol. Ecol. 13: 2235–2242.

Gabriel, A.G.A., S. L. Chown, J. Barendse, D. J. Marshall, R. D. Mercer, P.J.A. Pugh, and V. R. Smith. 2001. Biological invasions of Southern Ocean islands: the Collembola of Marion Island as a test of generalities. Ecography 24: 421–430.

Hartley, S., and P. J. Lester. 2003. Temperature-dependent development of the Argentine ant, *Linepithema humile* (Mayr) (Hymenoptera: Formicidae): a degree-day model with implications for range limits in New Zealand. N Z Entomol. 26: 91–100.

Hartley, S., R. J. Harris, and P. J. Lester. 2006. Quantifying uncertainty in the potential distribution of an invasive species: climate and the Argentine ant. Ecol. Lett. 9: 1068–1079.

Hartley, S., P. D. Krushelnycky, and P. J. Lester. 2010. Integrating physiology, population dynamics and climate to make multi-scale predictions for the spread of an invasive insect: the Argentine ant at Haleakala National Park, Hawaii. Ecography 33: 83–94.

Hee, J. J., D. A. Holway, A. V. Suarez, and T. J. Case. 2000. Role of propagule size in the success of incipient colonies of the invasive Argentine ant. Conserv. Biol. 14: 559–563.

Heller, N. E., and D. M. Gordon. 2006. Seasonal spatial dynamics and causes of nest movement in colonies of the invasive Argentine ant (*Linepithema humile*). Ecol. Entomol. 31: 499–510.

Heller, N. E., N. J. Sanders, J. W. Shors, and D. M. Gordon. 2008. Rainfall facilitates the spread, and time alters the impact, of the invasive. Argentine ant. Oecologia 155: 385–395.

Herbert, F. B. 1932. Effect of cold storage temperatures on the Argentine ant. J. Econ. Entomol. 25: 832–833.

Holway, D. A., A. V. Suarez, and T. J. Case. 2002a. Role of abiotic factors in governing susceptibility to invasion: a test with Argentine ants. Ecology 83: 1610–1619.

Holway, D. A., L. Lach, A. V. Suarez, N. D. Tsutsui, and T. J. Case. 2002b. The causes and consequences of ant invasions. Annu. Rev. Ecol. Syst. 33: 181–233.

Human, K. G., S. Weiss, A. Weiss, B. Sandler, and D. M. Gordon. 1998. Effects of abiotic factors on the distribution and activity of the invasive Argentine ant (Hymenoptera: Formicidae). Environ. Entomol. 27: 822–833.

Jumbam, K. R., S. Jackson, J. S. Terblanche, M. A. McGeoch, and S. L. Chown. 2008. Acclimation effects on critical and lethal thermal limits of workers of the Argentine ant, *Linepithema humile.* J. Insect Physiol. 54: 1008–1014.

Keller, L., and L. Passera. 1988. Energy investment in gynes of the Argentine ant *Iridomyrmex-Humilis* (Mayr) in relation to the mode of colony founding in ants (Hymenoptera, Formicidae). Int. J. Invertebr. Reprod. Dev. 13: 31–38.

Korzukhin, M. D., S. D. Porter, L. C. Thompson, and S. Wiley. 2001. Modeling temperature-dependent range limits for the fire ant *Solenopsis invicta* (Hymenoptera: Formicidae) in the United States. Environ. Entomol. 30: 645–655.

Krushelnycky, P. D., S. M. Joe, A. C. Medieros, C. C. Daehler, and L. L. Loope. 2005. The role of abiotic conditions in shaping the long-term patterns of a high-elevation Argentine ant invasion. Divers. Distrib. 11: 319–331.

Lester, P. J. 2005. Determinants for the exotic ants in New Zealand. Divers. Distrib. 11: 279–288.

Markin, G. P. 1970. Foraging behavior of the Argentine ant in a California citrus grove. J. Econ. Entomol. 63: 740–744.

McGeoch, M. A., P. C. Le Roux, E. A. Hugo, and S. L. Chown. 2006. Species and community responses to short-term climate manipulation: microarthropods in the sub-Antarctic. Aust. Ecol. 31: 719–731.

Menke, S. B., R. N. Fisher, W. Jetz, and D. A. Holway. 2007. Biotic and abiotic controls of Argentine ant invasion success at local and landscape scales. Ecology 88: 3164–3173.

Morrison, L. W., S. D. Porter, E. Daniels, and M. D. Korzukhin. 2004. Potential global range expansion of the invasive fire ant, *Solenopsis invicta.* Biol. Invasions 6: 183–191.

Moyle, P. B., and T. Light. 1996. Fish invasions in California: Do abiotic factors determine success? Ecology 77: 1666–1670.

Newell, W., and T. C. Barber. 1913. The Argentine ant. U.S.D.A. Bur. Entomol. No. 122. 98 p.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421: 37–42.

Roura-Pascual, N., A. V. Suarez, K. McNyset, C. Gomez, P. Pons, Y. Touyama, A. L. Wild, F. Gascon, and A. T. Peterson. 2006. Niche differentiation and fine-scale projections for Argentine ants based on remotely sensed data. Ecol. App. 16: 1832–1841.

SAS Institute. 2004. SAS 9.1.3 Help and Documentation. SAS Institute, Cary, NC.

SCAN. 2009. United States Department of Agriculture Soil Climate Analysis Site. (http://www.wcc.nrcs.usda.gov/scan/).

SCO. 2009. 1971–2000 Climate Normals. State Climate Office of North Carolina.

Silverman, J., and R. J. Brightwell. 2008. The Argentine ant: challenges in managing an invasive unicolonial pest. Annu. Rev. Entomol. 53: 231–252.

Simberloff, D., and B. Von Holle. 1999. Positive interactions of nonindigenous species: invasional meltdown? Biol. Invasions 1: 21–32.

Smith, M. R. 1919. Occurrence of the Argentine ant at Raleigh, North Carolina. J. Econ. Entomol. 12: 465.

Smith, M. R. 1928. The biology of *Tapinoma sessile* Say, an important house-infesting ant. Ann. Entomol. Soc. Am. 21: 307–330.

Smith, M. R. 1936. Distribution of the Argentine ant in the United States and suggestions for its control and eradication. Circ. U S Depart. Agric. 387: 1–39.

Stachowicz, J. J., R. B. Whitlatch, and R. W. Osman. 1999. Species diversity and invasion resistance in a marine ecosystem. Science 286: 1577–1579.

Suarez, A. V., D. A. Holway, and T. J. Case. 2001. Patterns of spread in biological invasions dominated by long-distance dispersal: insights from Argentine ants. Proc. Nat. Acad. Sci. U S A 98: 1095–1100.

Torchin, M. E., K. D. Lafferty, A. P. Dobson, V. J. McKenzie, and A. M. Kuris. 2003. Introduced species and their missing parasites. Nature 421: 628–630.

Walters, A. C., and D. A. Mackay. 2003. An experimental study of the relative humidity preference and survival of the Argentine ant, *Linepithema humile* (Hymenoptera, Formicidae): comparisons with a native *Iridomyrmex* species in South Australia. Insect Soc. 50: 355–360.

Walters, A. C., and D. A. Mackay. 2004. Comparisons of upper thermal tolerances between the invasive Argentine ant (Hymenoptera: Formicidae) and two native Australian ant species. Ann. Entomol. Soc. Am. 97: 971–975.

Williams, M. L., and M. Kosztarab. 1972. Morphology and systematics of the Coccidae of Virginia with notes on their biology. Vir. Poly. I. Res. Div. B. 74.

Witt, A.B.R., and J. H. Giliomee. 1999. Soil-surface temperatures at which six species of ants (Hymenoptera: Formicidae) are active. African Entomol. 7: 161–164.

Received 13 November 2009; accepted 23 June 2010.