

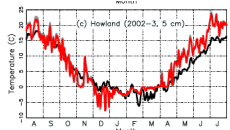


Constraints on cold tolerance and hardening limit the distribution of *Aphaenogaster picea* (Formicidae) at its northern range boundary

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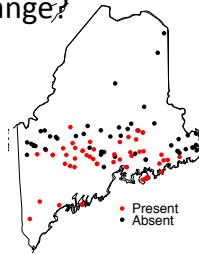
Common forest ants experience thermally stressful environments over long and short time scales.



Q1: What determines their distribution at their northern range?

H: Local climate conditions limit their northern range boundary.

Approach: 1) Sample presence absence in Maine; 2) Determine which climate variables best predict distribution.



Take home message: Forest ants display constraints in coping with extreme low temperatures and temperature variation, which likely limit their ability to persist past their northern range boundary.

Predictive modeling reveals that temperature and seasonality most likely limit their northern distribution.

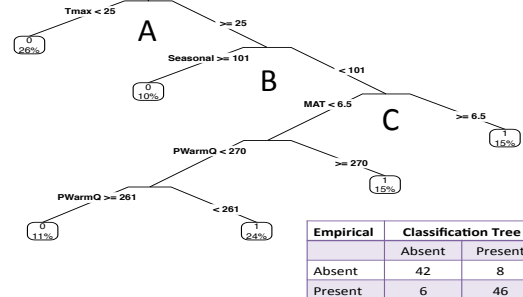


Fig1. Classification Tree Analysis displaying four important climate variables (Tmax, Seasonality, Mean Annual Temperature [MAT], Precipitation at warmest quarter [PWarmQ]; worldclim.org) that best predict the presence and absence of *A. picea* with a **86% accuracy**. Absences are represented by 0's and presences are 1's.

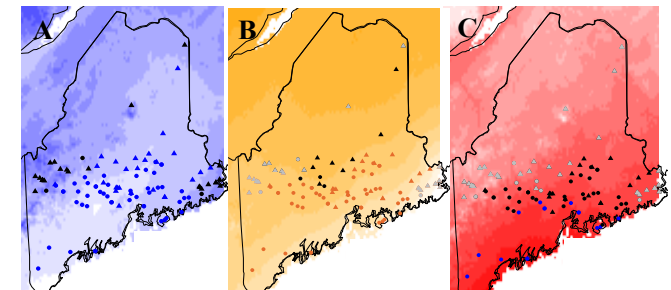
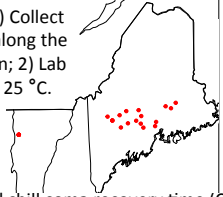


Fig2. Each panel displays the cutoffs for the first three nodes in Fig1 (A=Tmax, B=Seasonality, C= MAT). Circles and triangles represent empirical presences and absences, respectively. Splits based on the classification tree are colored and indicated for the first 3 nodes. **Black points indicates sites where the model predicts absence.** Grayed points indicate sites excluded from previous nodes. The background coloring shows gradient for that climate variable.

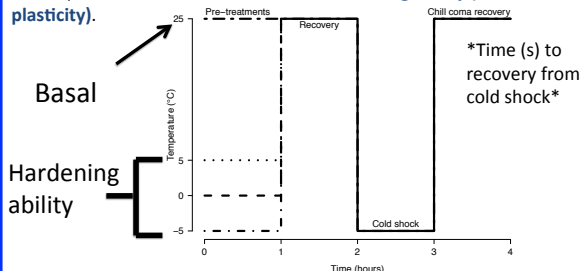
Q2: Are they physiologically constrained?

H: Forest ants have limited ability to cope with cold extremes and temperature variation.

Approach: 1) Collect forest ants along the range margin; 2) Lab acclimate at 25 °C.



3) Measured chill coma recovery time (CCRT) with different pre-treatments in a circulating water bath. 25 °C pre-treated ants represent **basal cold tolerance** and 5, 0, -5 °C pre-temperature treated ants represent three different levels of **hardening ability** (short term plasticity).



Evidence for trade-offs:
High basal cold tolerance = Low hardening ability

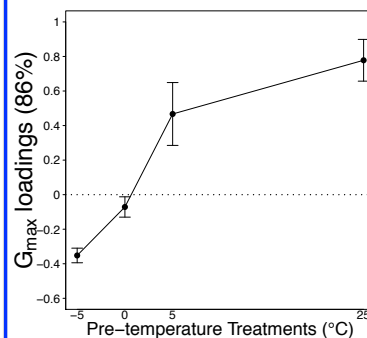


Fig3. Genetic correlation of cold tolerance among four pre-temperature treatments. We constructed a broad sense (colony level) variance-covariance (G-) matrix. We then determined the genetic orientation of each pre-temperature treatment with a principle component analysis (PCA). The first PC, Gmax, captured **86%** of the variation in G. G was also permuted 10 times to estimate variation in loading estimates.

Trade-offs are clinally structured:
Colonies from **cooler sites** have high basal tolerances and low hardening ability

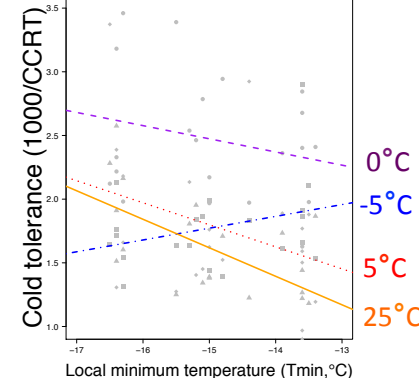


Fig4. Cold tolerances (1,000/CCRT) of forest ants clinally vary with local minimum temperatures (Tmin; $F_{1,57}=7.1$, $p<0.05$), and to different degrees depending on prior temperature exposure (Pre-treatment x Tmin; $F_{3,57}=3.8$, $p<0.05$). Colonies from cooler sites have high basal cold tolerances, but low hardening ability than colonies from warmer sites.

Summary: Cold adaptation involves shifting from plastic to constitutive mechanisms

Temperatures become **cooler** and more **variable** in more poleward locations:
* Selects for ants to operate under cold extremes and phenotypic plasticity

- 1) We identified a steep climate gradient for *A. picea*.
- 2) They are unable to overcome it due to constraints in cold physiology

Our study suggests that forest ants **fail to persist** past their northern range limit due to physiological constraints

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