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Impacts of Elevated Temperature on Ant Species, Communities and Ecological Roles at Two Temperate Forests in Eastern North America

Abstract: Over the course of five years we have established a long-term array of warming chambers at Duke and Harvard Forest that simulate future conditions with regard to temperature. In these chambers, we have studied, ants, other animal taxa, fungi, bacteria and plants and their responses to the treatments. We have coupled these studies with lab experiments, large-scale observations, and models to contextualize our results. Finally, we have developed integrative models of the future distribution of species and their consequences as a result of warming in eastern North America and more generally.

Amazingly, we have completed all of our proposed research to understand the effects of climatic change and in particular warming on the behavior, reproduction, population density, abundance, diversity and composition of ants and the ecosystem services mediated by ants but also of small animals more generally. Work from this project has resulted in a large numbers papers in press or published. We have also received additional grants to supplement this research from the National Science Foundation (for extrapolating our local results globally), the NCSU Global Change Forum (for communicating our results to the public), the EPA (for work on plant physiology) and NASA (for linking local observations and remote observations as relates to climate, climate change and insects).

The Big (5 m diameter) chambers

The core of our research focuses on our large-scale chamber manipulation of temperature in the forest understory at the northern and southern boundaries of the ranges of many species. We tracked the response of our focal taxon (ants) to this manipulation and also recorded responses of plants, beetles, spiders, collembola, mites, scales and other groups. In addition, we are conducted a suite of studies complimentary to our big chamber work. These complementary studies took advantage of global biogeographic approaches, laboratory common garden experiments, phylogenetic reconstructions, observational sampling and modeling of several forms.

During the first phase of our study, a major hurdle was installing infrastructure. But after a year we installed twelve climate chambers (5 m diameter circular chambers, centered on trees), manipulated to simulate four levels of warming (from ambient to + 5.5 degrees C) and three non-chamber control plots. The chambers themselves have now run at both sites for five years. At Harvard Forest all of the chambers have been constantly on since 9/30/09 and at Duke Forest the chambers have been on since 12/03/09. The warmest chambers are maintained at +5.5 degrees C. The chambers have been remarkably consistent in terms of their treatment effects.

Baiting and pitfall studies---We have conducted monthly baiting surveys of ants and pitfall samples in every chamber over the course of the entire year. Baiting has focused on sampling ants during the day, but once each month each chamber is surveyed for twenty-four hours. With warming, day foraging ants are shifting to the night and those that rely on cool night temperatures are becoming more rare. We can now predict which ants respond favorably to warming, which become rare and have tested these predictions using long-term historical data, observational geographic data, physiological models and other approaches.

Plant phenologies—Along with sampling ants, we also sampled plants in the chambers. In all chambers, 1x1 m quadrats were established just inside the first entrance to the right of the blower. The quadrats were setup to the left of the opening (to allow easy ingress and egress to the chamber). All plants <2cm in diameter in the quadrats have been sampled monthly. In the initial census, all plants present were individually tagged with a bird band and their number. In the first and subsequent censuses, height (ground to highest apical bud), number of leaves, types of herbivory incurred, percentage of leaf area damaged by herbivory, types and levels of pathogen incidence (description of symptoms and % leaf area covered), any insects encountered, presence of dried leaves, and any instances where leaves were

attached to other leaves (a.k.a. "pinned") via insect-generated structures (particularly web-spinning Lepidoptera) were all recorded. Plant phenology has shifted roughly three weeks earlier and later in the warmest chambers relative to the controls. For a subset of plant species, we can contextualize these shifts with detailed physiological observations and models.

Other taxa—Two of our methods, pitfall sampling and winkler sampling, sample ants, but also other taxa. We have enlisted collaborators to identify specimens of other taxa (and in some cases, study them in more detail) as they are extracted from these traps. Our collaborators have studied spiders, millipedes collembola, mites, beetles, aphids and scale insects, bacteria and fungi.

Work outside the big chambers

Regional and global distribution--We have modeled the distribution of ant species in North America and ant genera globally in the context of global climate change. This work gives us better and better predictions of how at a large scale species' distributions are likely to change, but it also allows us an effective framework for the integration of observational data and experimental results. As a consequence of work earlier funded by DOE NICCR, we now have maps available online of all North American ant species and all ant genera globally, which have led to numerous collaborative spin off projects on the distribution of particular clades and functional groups and a current effort to model predation by ants geographically. Clinton Jenkins, for example, examined the consequences of warming at the global spatial extent for local ant assemblages and the processes they mediate (Jenkins et al. in revision). Michael Weiser examined the extent to which knowledge of ground ant assemblages helps (or does not help) predict the composition and abundance of canopy ant assemblages. Sean Menke, at Lake Forest College, worked with us to understand whether the response of species to experimental warming can be used to predict the response of species to urban intensification and heat islands (Menke et al. 2010).

***Mini chambers* --**In order to better understand the range of scenarios that are possible in the context of warming for ants in a setting that allows greater replication and a wider variety of treatments, we installed passive warming and cooling mini chambers at each of the two field sites (Harvard Forest and sites in the piedmont of North Carolina). The mini chambers consisted of PVC frames covered in shade cloth (cooling) or greenhouse plastic (warming) and achieved a mid-day change in temperature of approximately 1.0 degrees C in both cases. Our first step in using these mini chambers was simply to observe changes in the composition of ant assemblages during summer months and how those changes affected ecological processes performed by ants: predation, seed dispersal, scavenging, nectivary, granivory. At our southern site, a single ant species took over the warm chambers, with consequences for a variety of ecological processes. At the northern site, we have not yet seen much change (similar to our observations in the big chambers). Later, we added a precipitation manipulation to these chambers to allow us to disentangle the effects of warming and drying on ants. With precipitation and warming, we have seen an increase in the abundance of a medically dangerous invasive species, *Pachycondyla chinensis*.

Models of ant and ant-dispersed plant demographics--In order to better understand the consequences of changes in assemblage structure due to climatic change on species that depend on ants in general or on species ant species, we developed dispersal models for the ant-dispersed plant, *Hexastylis arifolia*. In these models, we considered the consequences of changes in the abundance of the ant *A. rudis* on rates of spread and population growth of *H. arifolia* (little brown jug). In short, even modest changes in the abundance of *A. rudis* can lead to decreases in population growth rates and rates of spread for *H. arifolia*. In addition, building on these first models we are now modeling the consequences of changes in climate on *A. rudis* and *H. arifolia* and on their population dynamics.

More recently, Judith Canner used simulation models to explore the dynamics of ants and ant-dispersed plants when confronted with immediate warming (as in a press experiment such as ours) or long-term warming. Judith found that with modest increases in temperature (up to +4 C), the results of immediate and long-term warming were similar. However, at even higher temperatures the results of immediate and long-term warming began to diverge, suggesting caution when interpreting the results of our warmest chambers in light of long-term trends.

Thermal tolerance -- Identifying characteristics of organisms that determine their sensitivity to climate change is crucial for ecological forecasting and conservation planning. The impact of increasing temperatures on species is likely to vary as functions of geography, physiology and shared evolutionary history. However, few attempts have been made to integrate these components into a single mechanistic framework. Importantly, constructing such a framework allows us to develop a predictive model for the magnitude and global distribution of species' responses to climate change. We have developed a predictive model for the determinants of critical thermal maxima (the upper lethal temperature, an important constraint on species' ability to withstand temperature increases) for ant species from around the world, based on climatic variables, life history traits and shared evolutionary history. This model has aided in identifying those species that will be most strongly affected by current and future climate change.

Our second step has been to apply the conceptual framework we have used to consider the world to our warming chambers: for both the Harvard and Duke Forest warming sites, we have examined whether critical thermal maxima predict which ant species are present across the warming treatments. At Duke Forest, critical thermal maxima are strong predictors of the distribution of ants among the warming treatments; in contrast, at Harvard Forest, critical thermal maxima have little ability to predict the distribution of ant species. These results suggest that species at higher latitudes (i.e. those at Harvard Forest) may be less impacted by climate change, as they are farther from their thermal optima (and thus their critical thermal maxima), compared to species at lower latitudes (i.e. those at Duke Forest).

Laboratory common garden experiment and ant thermal tolerance – Common garden experiments are morally questionable in the field with ants, but straightforward in the lab. We have performed multiple long-term (4 month) common garden laboratory-based study at NCSU (Phytotron growth chamber facility) to more fully dissect the contribution of geography to species' responses to climate change. Common ant species including *Aphaenogaster rudis*, *Temnothorax curvispinosis*, *Tapinoma sessile*, and *Crematogaster lineolata* were obtained from areas around the Harvard and Duke Forest warming sites,

and each was replicated across one of three temperature treatments (fluctuating temperature treatments matching mean summer temperatures in Harvard Forest, Duke Forest, and a more Southerly point in Florida as a proxy for future climate warming conditions). Data on colony survival, brood production, running speed, and immune function were obtained. Analyses suggest strong species-specific responses. For example, *A. rudis* could not forage sufficiently to maintain their increased metabolism under the warmest treatment, and all colonies died within the first week of the experiment, while other species had nominal performance at this stage. Overall, geographic signal was relatively weak compared to phylogenetic signal (species-specific responses) and the main effect of temperature (colony performance was diminished with increased warming).

Running speed studies---We have collaborated with Lauren Buckley and Heidi MacClean at the University of North Carolina to conduct tests of thermal performance curves for ants subjected to both chamber and phyototron warming treatments. To date, evidence from the phytotron suggests very little local adaptation (but strong aclimitization) of southern populations of widespread species to warmer southern temperatures.

Fungal pathogen challenge—Ants from both chamber and phytotron experiments have been challenged with fungal pathogens to look at the effects of warming on both immune defense levels and on colony level susceptibility to pathogens.

Publications

Meineke, E. K., Dunn, R. R., Frank, S. D. (2014) Early pest development and loss of biological control are associated with urban warming. *Biology Letters*. doi: 10.1098/rsbl.2014.0586.

Youngsteadt, E., Dale, A. G.*, Terando, A. J., Dunn, R. R. and Frank, S. D. (2014). Do cities simulate climate change? A comparison of herbivore response to urban and global warming. *Global Change Biology*. doi: 10.1111/gcb.12692.

Guenard, B.*, Cardinal-De Casas**, A, Dunn, RR (2014). High diversity in an urban habitat: are some animal assemblages resilient to long-term anthropogenic change? *Urban Ecosystems*. DOI 10.1007/s11252-014-0406-8.

Bewick, S., Stuble, K.L.*, Lessard, J. P., Dunn RR, Adler, F. R., Sanders, N. J. (2014). Predicting future coexistence in a North American ant community. *Ecology and Evolution* 4 (10), 1804-1819. View PDF.

Cregger MA*, Sanders NJ, Dunn RR, and Classen AT (2014). Microbial communities respond to experimental warming, but site matters. *PeerJ* 2:e358.

Stuble KL*, Patterson CM**, Rodriguez-Cabal MA*, Ribbons RR*, Dunn RR, Sanders NJ (2014). Ant-mediated seed dispersal is resistant to extreme experimental warming. *PeerJ* 2, e286.

Resasco J*, Pelini SL, Stuble KL*, Sanders NJ, Dunn RR, Ellison AM, Gotelli NJ, Levey DJ (2014). Using historical and experimental data to reveal warming effects on ant assemblages. *PLoS One* 9:e88029.

Burt MA*, Nichols LM, Dunn RR, Sanders NJ (2014). Interactions in a warmer world: effects of experimental warming, conspecific density, and herbivory on seedling dynamics. *Ecosphere* 5:9.

Menke, SB, Harte, J, Dunn RR (2014). Changes in ant community composition caused by 20 years of experimental warming vs. 13 years of natural climate shift. *Ecosphere*. 5:1.

Diamond, S. E., C. Penick, S. L. Pelini, A. M. Ellison, N. J. Gotelli, N. J. Sanders, and Dunn RR. (2013). Using physiology to predict the responses of ants to climatic warming. *Integrative and Comparative Biology* 53:965-974. View PDF.

Stuble KL*, Pelini SL, Diamond SE, Fowler DA**, Dunn RR, Sanders NJ (2013). Foraging by forest ants under experimental climatic warming: a test at two sites. *Ecology and Evolution* 3:482-491. View PDF.

Stuble KL, Rodriguez-Cabal MA, McCormick GL, Jurić I, Dunn RR, et al. (2013). Tradeoffs, competition, and coexistence in eastern deciduous forest ant communities. *Oecologia* 171: 981-992. View PDF.

Meineke EK*, Dunn RR, Sexton JO, Frank SD (2013). Urban Warming Drives Insect Pest Abundance on Street Trees. *PloS ONE* 8: e59687.

Jenkins CN, Guénard B, Diamond SE, Weiser MD, Dunn RR (2013). Conservation implications of divergent global patterns of ant and vertebrate diversity. *Diversity and Distributions* 19(8): 1084-1092. View PDF.

Canner JE*, Dunn RR, Giladi I, Gross K (2012) Redispersal of seeds by a keystone ant augments the spread of common wildflowers. *Acta Oecologica* 40: 31-39. View PDF.

Diamond SE, Nichols LM, McCoy N, Hirsch C**, Pelini SL, Dunn RR (2012) A physiological trait-based approach to predicting the responses of species to experimental climate warming. *Ecology* 93: 2305-2312. View PDF.

Diamond, S. E., D. M. Sorger*, J. Hulcr, S. L. Pelini, I. Del Toro*, C. Hirsch**, E. Oberg, and Dunn RR. 2012. Who likes it hot? A global analysis of the climatic, ecological, and evolutionary determinants of warming tolerance in ants. *Global Change Biology*18:448-456. View PDF.

Pelini SL, Diamond SE, MacLean H*, Ellison AM, Gotelli NJ, Dunn RR (2012) Common garden experiments reveal uncommon responses across temperatures, locations, and species of ants. *Ecology and Evolution* 2: 3009-3015. View PDF.

Rodriguez-Cabal MA*, Stuble KL*, Guénard B, Dunn RR, Sanders NJ. (2012) Disruption of ant-seed dispersal mutualisms by the invasive Asian needle ant (*Pachycondyla chinensis*). *Biological Invasions* 14(3): 557-565. View PDF.

Dunn RR, Fitzpatrick MC (2012) Every Species Is an Insect (or Nearly So): On Insects, Climate Change, Extinction, and the Biological Unknown. Saving a Million Species: Island Press/Center for Resource Economics. pp. 217-237.

Guénard B, McCaffrey KA, Lucky A, Dunn RR (2012) Ants of North Carolina: an updated list (Hymenoptera: Formicidae). *Zootaxa*3552: 1-36.

Guénard B, Weiser MD, Dunn RR (2012) Global models of ant diversity suggest regions where new discoveries are most likely are under disproportionate deforestation threat. *Proceedings of the National Academy of Sciences* 109: 7368-7373. View PDF.

Jenkins, C. + 22 authors, Dunn, R. R. 2011. Global diversity in light of climate change: the case of ants. *Diversity and Distributions*. 17: 652-662.

Machac, A., Janda, M., Dunn, R. R., and N. J. Sanders. 2011. Elevational gradients in phylogenetic structure of ant communities reveal the interplay of biotic and abiotic constraints on diversity. *Ecography*. 34: 364-371.

Menke, S. B., Guenard, B., Sexton, J., Silverman, J. and Dunn, R. R. 2011. Urban areas may serve as habitat and corridors for dry-adapted, heat tolerant species; an example from ants. *Urban Ecosystems* 14: 135-163.

Gotelli, N. J., Ellison, A. M., Dunn, R. R., and N. J. Sanders. 2011. Counting ants (Hymenoptera: Formicidae): biodiversity sampling and statistical analysis for myrmecologists. *Mymecological News*. 15: 13-19.

Pelini, S. L., Boudreau, M., McCoy, N., Ellison, A. M., Gotelli, N. J., Sanders, N. J., Dunn, R. R. 2011. Effects of short-term warming on low and high latitude forest ant communities. *Ecosphere* 2: art62.

Pelini, S. L., Bowles, F. P., Ellison, A. M., Gotelli, N. J., Sanders, N. J., Dunn, R. R. 2011. Heating up the forest: open-top chamber warming manipulation of arthropod communities at Harvard and Duke Forests. *Methods in Ecology and Evolution* : doi: 10.1111/j.2041-210X.2011.00100.

Diamond, S. E., D. M. Sorger, J. Hulcr, S. L. Pelini, I. Del Toro, C. Hirsch, E. Oberg, and R. R. Dunn. Who likes it hot? A global analysis of the climatic, ecological, and evolutionary determinants of warming tolerance in ants. *Global Change Biology*.

Fitzpatrick MC, Sanders NJ, Ferrier S, Longino JT, Weiser MD, Dunn RR (2011) Forecasting the future of biodiversity: a test of single- and multi-species models for ants in North America. *Ecography*.

Zelikova TJ, Sanders NJ, Dunn RR (2011) The mixed effects of ants on above and belowground processes in a temperate forest.*Ecosphere* 2(5): 63

Gotelli, Nicholas J., Aaron M. Ellison, Robert R. Dunn, and Nathan J. Sanders. Forthcoming. Counting ants (Hymenoptera: Formicidae): Biodiversity sampling and statistical analysis for myrmecologists. *Myrmecological News* 15:13-19.

McGlynn, T., M. D. Weiser, and R. R. Dunn. 2010. More individuals but fewer species: testing the 'more individuals hypothesis' in a diverse tropical fauna. *Biol. Lett*. published online before print March 3, 2010, doi:10.1098/rsbl.2010.0103

Weiser, M. D., Sanders, N. J., Agosti, D., Andersen, A. N., Ellison, A. M., Fisher, B. L., Gibb, H., Gotelli, Gove, A. D., Gross, K., Guenard, B., Janda, M., Kaspari, M., Lessard, J. P., Longino, J. T., Majer, J. D., Menke, S. B., McGlynn, T. P., Parr, C. L., Philpott, S. M., Retana, J., Suarez, A. V., Vansconcelos, H. L., Yanoviak, S. P. and R. R. Dunn. 2010. Canopy and litter ant assemblages share similar climate–species density relationships. *Biol. Lett*. published online before print May 12, 2010, doi:10.1098/rsbl.2010.0151

Menke, SB, Guénard B, Sexton JO, Weiser MD, Dunn RR, Silverman J (2010). Urban areas may serve as habitat and corridors for dry-adapted, heat tolerant species; an example from ants. *Urban Ecosystems*.

R.R. Dunn, N.J. Sanders, B. Guénard and M.D. Weiser. 2009. Geographic gradients in the diversity, abundance, size, and ecological consequences of ants. Ant Ecology, L. Lach C. Parr and K. Abbot, editors (Invited). Oxford University Press.

Sanders NJ, Dunn RR, et al. 2009. A diversity of elevational diversity gradients. In Data mining for global trends in mountain biodiversity Edited by Körner C and Spehn E (Invited).

Dunn, R.R., N.J. Sanders, S.B. Menke, M.D. Weiser, M.C. Fitzpatrick, E. Laurent, J.-P. Lessard, D. Agosti, A. Andersen, C. Bruhl, X. Cerda, A. Ellison, B. Fisher, H. Gibb, N. Gotelli, A. Gove, B. Guénard, M. Janda, M. Kaspari, J.T. Longino, J. Majer, T.P. McGlynn, S.B. Menke, C. Parr, S. Philpott, M. Pfeiffer, J. Retana, A. Suarez, H. Vasconcelos. 2009. Climatic Drivers of Hemispheric Asymmetry in Global Patterns of Ant Species Richness. *Ecology Letters*.