

# Interacting effects of urbanization and coastal gradients on ant thermal responses

R.J. Warren II,\* S. Bayba and K.T. Krupp

Department of Biology, SUNY Buffalo State, 1300 Elmwood Avenue, Buffalo, NY 14222, USA

\*Corresponding author. E-mail: hexastylis@gmail.com

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## Abstract

Urban-to-rural gradients intersect with other, often unmeasured, environmental gradients that may influence or even supersede species responses. Here we use coastal-to-interior and urban-to-rural gradients to investigate woodland ant response (physiological thermal tolerance, community structure and spring phenology) to two overlapping thermal gradients, the Great Lakes (Erie and Ontario) and the Buffalo, NY urban center (USA). Woodland ant physiological and behavioral responses, and community responses, shifted along the coastal-to-interior and urban-to-rural gradients, but they were generally best explained by lake effects (though urban ants tolerated higher temperatures than rural ants). The relatively colder spring temperatures in coastal areas (as compared with inland) corresponded with higher physiological cold tolerance in the ants, even though the coastal areas are annually warmer. The coastal spring temperatures also influenced ant phenology so that, in a warm year, the coastal ants began foraging considerably earlier than inland ants, likely due to their lower physiological cold tolerance. Ant community responses also shifted with proximity to the lakes and urban areas, but those changes appeared more linked with land use than climate. These results suggest that species responses to urbanization gradients may be influenced, or even superseded, by the impacts of proximate large water bodies. Our results suggested that spring coldness nearer the Great Lakes may select for cold tolerance in ants (despite that the coastal areas are relatively warmer annually), whereas urbanization selected for greater heat tolerance.

**Key words:** *Aphaenogaster rudis*,  $CT_{min}$ ,  $CT_{max}$ , gradient study, Great Lakes

## Introduction

Climatic gradients provide a template on which researchers use correlations between environmental drivers and corresponding biotic responses to make inferences about underlying ecological and evolutionary processes (Whittaker 1978; McDonnell and Pickett 1990; Ibanez et al. 2013). A long-term tradition in ecological research is the use of elevation gradients to capture shifts in temperature and precipitation, and associated biota, but more recently urbanization gradients are used to capture spatial shifts in anthropogenic impact (Whittaker 1956, 1978; McDonnell and Pickett 1990). Less common are coastal-to-interior gradient studies that examine the impacts of large bodies of water on proximate terrestrial environments (Osland, Enwright and Stagg 2014; Wong et al. 2015; Tayyebi and Jenerette 2016). Approximately half of the US population lives on the coasts of the Great Lakes, Atlantic

Ocean or Pacific Ocean, and species responses to urbanization gradients in these areas may be influenced by large water bodies.

Whereas ‘gradient’ implies predictable shifts, ecological responses often are not so. For example, in the Great Lakes region (North America), many fruit trees grow in climate refuges far north of their main growing zones because the large water bodies moderate proximate terrestrial temperatures throughout the year (Day 1832; Eichenlaub 1979; Scott and Huff 1996). However, these ‘moderating’ effects are not straightforward as the coastal-to-interior gradients generally invert during annual cycles so that spring cooling prevents early budding and autumn warming prevents early killing frosts relative to the inland, mid-continental region (Day 1832; Eichenlaub 1979; Scott and Huff 1996). Hence, ecological responses may reflect annual temperature extremes or the seasonal interactions between temperature shifts and critical life history stages, making Great

Lakes coastal-to-interior climatic gradients ideal for studying the complexities of ecological climatic responses.

Seasonal and geographical variation in temperature shapes the responses and distribution of ecological communities (Jeffree and Jeffree 1994; Tewksbury, Huey and Deutsch 2008; Warren and Chick 2013), particularly ectothermic organisms whose body temperature is dependent on ambient conditions (Deutsch et al. 2008; Diffenbaugh and Field 2013; Kingsolver, Diamond and Buckley 2013). Small ectotherms essentially track ambient temperature with their body temperature and physiology, making them particularly sensitive to the thermal environment (Stevenson 1985; Hochachka and Somero 2002; Paaijmans et al. 2013). Insects are the most diverse, widespread and functionally variable ectotherm, labeled 'thermal warriors' for the vast and varied adaptations they have evolved to regulate body temperature (Heinrich 1996). Ants make excellent study organisms for climatic gradient research because they are abundant, ubiquitous and diverse; behaviorally and physiologically varied (generally thermophilic); limited in distribution and behavior by temperature; key biotic components of most terrestrial ecosystems; and well-studied for thermal tolerances, biotic interactions and community composition drivers (Hölldobler and Wilson 1990; Albrecht and Gotelli 2001; Wittman et al. 2010; Zelikova, Sanders and Dunn 2011; Warren and Chick 2013; King, Warren and Bradford 2013; Diamond et al. 2017b).

Ant species sort out along latitude, elevation and land use gradients, exhibiting species-specific behavioral and physiological responses to temperature which, in turn, influence ant interactions and community structure (Angilletta et al. 2007; Sanders et al. 2007; Dunn et al. 2009; Stuble et al. 2013; Kaspari et al. 2016; Diamond et al. 2017a). Ant species richness generally increases with temperature, with higher species richness at lower latitudes and altitudes (Dunn, Parker and Sanders 2007; Lessard et al. 2007), but at smaller scales, such as along elevation gradients, ant richness may actually reverse or peak at intermediate temperatures (Sanders, Moss and Wagner 2003; Dunn et al. 2009; Longino and Colwell 2011), likely due to shifts in land use. For instance, ant species richness can be unexpectedly high in urban areas, even higher than forested habitat (Lessard and Buddle 2005). Disturbance-tolerant, open-habitat species, may succeed in urban areas because of the heterogeneity of habitats, and because they can utilize small patches such as abandon lots, forest fragments and pavement medians (Uno, Cotton and Philpott 2010; Guénard, Cardinal-De Casas and Dunn 2015). However, in the deciduous forest biome of North America (NA), ant species richness generally is higher in forested than proximate urban habitat (Uno, Cotton and Philpott 2010; Guénard, Cardinal-De Casas and Dunn 2015; Crist and Kaitlin 2017).

Ant phenology (e.g. the timing of the end of winter diapause, initiation of foraging and mating flights) also shifts along environmental gradients, initiated by increasing temperature (Warren and Chick 2013). Many ant interactions with plants and animals depend on phenological timing (Fujiwara et al. 2013; Warren and Giladi 2014), which is mediated by spring temperatures (Pelini et al. 2012; Stuble et al. 2013; Warren and Bradford 2014). For example, in eastern NA, ant-dispersed woodland plant seed release corresponds with early spring foraging by ants in the *Aphaenogaster* genus, the primary seed dispersers in these habitats (Ness, Morin and Giladi 2009; Warren and Bradford 2014). A temperature difference of  $\sim 2^{\circ}\text{C}$  corresponds with substantial shifts in ant behavior and community responses, and can result in failed synchronicity with interacting species (Wittman et al. 2010; Lessard et al. 2011; Warren and Bradford 2014).

Our objective was to investigate woodland ant physiological (minimum and maximum temperature tolerance), behavioral

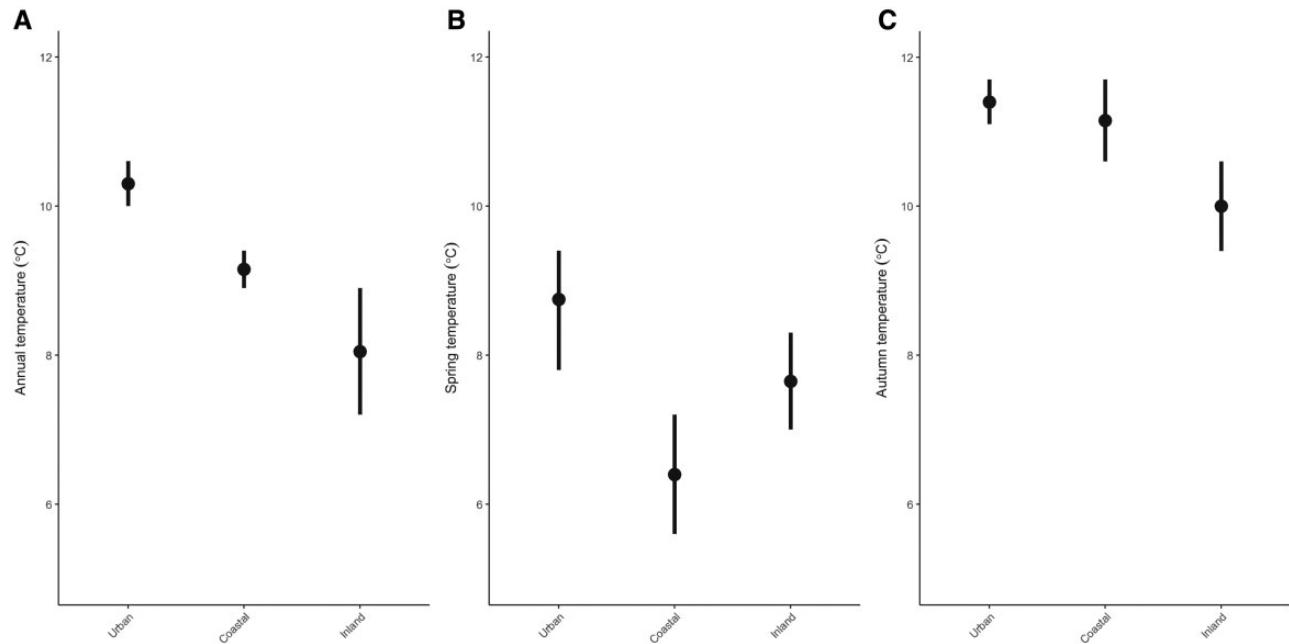
(spring foraging phenology) and community (species richness) responses to two Great Lakes (Erie and Ontario) and the Buffalo, NY urban center in Western New York (WNY) State (USA). If the lake effect is an overall moderating force on proximate terrestrial temperatures, (H1) we expected that the woodland ants nearest to the lakes would be less cold tolerant and have a narrower range of temperature tolerance than further inland. Great Lakes thermal effects can invert during annual seasons, however, so that coastal areas are relatively colder in spring and warmer in autumn (Day 1832; Eichenlaub 1979; Scott and Huff 1996). Given that key ant life history stages (such as the breaking of winter diapause and brood development) occur in early spring, (H2) ants near the Great Lakes may have greater cold tolerance and an overall wider range of thermal tolerances than inland ants. Urban areas often create 'heat islands' that also in narrow temperature ranges due to warmer nights and winters (Imhoff et al. 2010; Ward et al. 2016; Hamblin et al. 2017). If the urban heat island effect overwhelms the lake effect, (H3) we expected less cold tolerance and greater heat tolerance in ants nearer the city center along the urban-to-rural gradient. We used woodland ant species richness and spring foraging phenology to further elucidate ant dynamics along the coastal-to-interior and urban-to-rural climatic gradients.

## Methods

### Study area and species

Western New York (WNY) is bordered by Lake Erie (25 700 km<sup>2</sup> area; 489 km<sup>3</sup> volume) to the West and Lake Ontario (18 960 km<sup>2</sup>; 1639 km<sup>3</sup>) to the North, two of the largest freshwater lakes in the world (by area and volume). Given that the predominant weather systems move easterly, and cold and icy water persists into spring, these large water bodies exert considerable effect on WNY temperature and precipitation (Day 1832; Eichenlaub 1979; Scott and Huff 1996). Western New York climatic gradients are formed by proximity to Lakes Erie and Ontario (coastal zones), the Buffalo urban area (urban) and inland geologic uplift south of Lake Ontario and east of Lake Erie (Vermette 2017a,b) [Supplementary Material S1]. Annually, the urban zone is warmest and inland zones coldest (Fig. 1A); however, in spring, the coastal zone is coldest, (Fig. 1B), and in autumn the coastal zone is relatively warmer, similar to the urban zone (Fig. 1C). Buffalo, NY is located on the shore of Lake Erie, approximately 45 km south of Lake Ontario, and it is the primary urban center of WNY (Supplementary Material S1) with a population of 257 000 and a city area of 136.0 km<sup>2</sup>. We used 35 municipal, state and federal parks and urban forest patches in WNY at varied distances from the lakes (0.1–58 km) and city center (0.1–60 km) to investigate ant physiological, behavioral and community responses to seasonal coastal-to-interior and urban climatic gradients (Supplementary Material S1).

Landscape gradients can cross many ecotones unrelated to the putative drivers. For example, urban-to-rural gradients may include forests or agriculture at the rural end, two highly disparate influences on ecological diversity (Warren et al. 2018). For this reason, we only sampled ants in wooded areas to standardize the study sites. Preliminary sampling indicated that *Aphaenogaster* ants [mostly *Aphaenogaster picea* (Wheeler, W.M., 1908)] were relatively ubiquitous at the woodland sites, which meant that they consistently occurred along the study gradients, and this genus is relatively easy to identify in the field, so we targeted it for thermal tolerance and spring phenology sampling. Moreover, ants in the *Aphaenogaster* genus are the most abundant/dominant ants in eastern deciduous forests



**Figure 1:** Median ( $\pm$ range) temperatures for WNY climate zones as compiled by Vermette (2017b). The urban zone essentially contains the greater Buffalo metropolitan area. The coastal zone includes lands immediately south of Lake Ontario and east of Lake Erie. The inland zone includes those climate zones furthest from the Great Lakes. Annually, the urban zone is warmest, followed by the coastal and then inland (A). However, due to the Great Lakes thermal influence, the coastal zone is cooler than the inland zone in the spring (B), but warmer in the autumn (C)

(Lubertazzi 2012; King, Warren and Bradford 2013) so a solid body of work exists on thermal responses of the *Aphaenogaster rudis* complex (Warren and Chick 2013; Pelini et al. 2014; Nguyen 2017).

Climatic influences on the interactions between species may be more important to ecological systems than the individual effects of climate on each species (Angert, LaDeau and Ostfeld 2013; Post 2013; Warren and Bradford 2014). As the dominant ant in eastern deciduous forests, *Aphaenogaster* species are key members of these ecosystems. They are the main food for terrestrial salamanders (Paluh et al. 2015), which themselves are the dominant vertebrate in these systems (Burton and Likens 1975). *Aphaenogaster* ants also influence forest ecosystem processes, such as decomposition through negative interactions with termites and wood-rot fungi (Bradford et al. 2014; Warren and Bradford 2014), and their climate-initiated dispersal of woodland plant seeds (Ness, Morin and Giladi 2009) is crucial for the distribution and survival of a large portion of forest understory plant biodiversity (Ness, Morin and Giladi 2009; Warren, Giladi and Bradford 2014).

### Minimum and maximum temperature tolerances

The physiological thermal limits of ectothermic organisms reflect their sensitivity to temperature extremes which, in turn, provides insight into their putative fitness and geographic distributions in response to climate (Huey and Kingsolver 1989; Terblanche et al. 2011; Sunday, Bates and Dulvy 2012). Thermal tolerance is a commonly used trait that essentially delineates the lower (critical thermal minimum, 'CT<sub>min</sub>') and/or upper (critical thermal maximum, 'CT<sub>max</sub>') physiological temperature limits for an organism—often measured as the sub-lethal thermal limit at which motor function fails, sometimes referred to as 'knock-down resistance' (Huey and Stevenson 1979). Knock-down resistance can be influenced by ant health (Terblanche

et al. 2011; Nguyen 2017) and the rate of ramping temperature up or down may impact some organisms (Terblanche et al. 2011), though Diamond et al. (2017a) found that the ramping up speed is unimportant for ants. Ants also may behaviorally acclimate to temperatures exceeding their thermal limits by limiting foraging to optimal periods and by moving nests to tolerable microhabitats (Smallwood 1982; McGlynn et al. 2010; Warren, Giladi and Bradford 2012). And, finally, key nonimmobilizing responses, such as reproduction, may be limited at temperatures less extreme than knock-down resistance (Jørgensen, Sørensen and Bundgaard 2006; Hoffmann 2010). Despite these limitations, knock-down resistance repeatedly has been linked with ant behavior and distribution. For example, greater heat tolerance corresponds with increased abundance, activity, running speed and brood development in higher temperatures [e.g. experimental warming, decreased elevation, increased urbanization] (Angilletta et al. 2007; Diamond et al. 2012a,b; Stuble et al. 2013; Kaspari et al. 2016; Penick et al. 2017) and greater cold tolerance, which is not as well-studied, corresponds with earlier foraging and greater activity in lower temperatures (Warren and Chick 2013; Bishop et al. 2017). These heat and cold tolerances correspond with shifts in ant community responses along temperature gradients consistent with sorting between relatively tolerant or intolerant species (Warren and Chick 2013; Penick et al. 2017).

We sampled live ants from 42 ant colonies at 28 of the 35 study sites in the WNY region [May–July 2016] (Supplementary Material S1). The study sites used for thermal sampling ranged in size from approximately 2–4000 ha of forested area. We minimized spatiotemporal confounding by sampling sites randomly throughout the summer so that sampling sequence did not follow either gradient or geographic proximity. We collected 15 ants each from two *Aphaenogaster* colonies at each site, except for five small parks with <10 ha of wooded area at which we collected one colony each. One colony sample was lost in

transport. In the northern portion of their range, *A. rudis* ants are darkly colored (much less red than the southern portion of their range) similarly to *A. picea*, so definitive identification was not made until after collection.

The ants were immediately placed individually into 16 mm glass test tubes filled with some nest soil and plugged with moistened cotton to maintain humidity and reduce stress. The cotton plugs also reduced movement during subsequent thermal testing. The field-collected test tubes were placed in racks and in a cooler with ice to prevent overheating during transport to the laboratory (with an insulator between the test tube racks and ice). Thermal testing was done on the same day as collection. From each 15-ant sample, ants were randomly assigned, five each, to  $CT_{max}$ ,  $CT_{min}$  and a control. A mean temperature for the loss of righting response served as the index for thermal tolerance for each sample at each site. A control sample of five ants from each colony was kept in the same test tube conditions as the thermal tolerance samples except that they were not put in the water bath. None of the control specimens lost their righting response during the testing. After thermal tolerance testing was completed, all ants were cataloged and stored in the Warren laboratory at the SUNY Buffalo State.

For  $CT_{max}$  (heat tolerance), we pre-warmed an Ac-150-A40 refrigerated water bath (NesLab, ThermoScientific, Portsmouth, NY, USA) to 30°C. We placed five test tubes with ants into the bath and allowed them to equilibrate for 10 min, at which point the temperature was increased by  $1.0^{\circ}C \text{ min}^{-1}$ . The ants were checked for 60 s after the unit reached the next temperature interval. At every interval, the ants righting responses were observed by lifting each test tube out of the bath very briefly. If the individual was immobile, the test tube would be turned and tapped to verify the ability to stay upright. Once an individual lost their ability to right it was removed, and the corresponding interval temperature recorded. Testing concluded after all individuals in a sample lost the ability to right themselves. For  $CT_{min}$  (cold tolerance), the water bath was precooled to 20°C, and the ants were allowed to equilibrate for 10 min. After the adjustment period, the temperature was decreased  $1.0^{\circ}C \text{ min}^{-1}$ , and the same procedure was followed as  $CT_{max}$ .

### Community responses

Timed searches were conducted haphazardly in wooded areas at all 35 sites in the WNY region [May–July 2017] (Supplementary Material S1), to assess ant species richness. At each site, downed logs and rocks were overturned and litter visually searched for ant colonies and individuals for 40 min (to standardize sampling across parks). Ants were collected with aspirators (3–4 representative individuals for colonies) for later identification (Fisher and Cover 2007; Ellison et al. 2012). All ants were cataloged and stored in the Warren laboratory at the SUNY Buffalo State. Whereas comprehensive ant community sampling often utilizes pitfall traps and leaf-litter extraction, woodland ant species typically aggregate in downed wood and rocks (Hölldobler and Wilson 1990; King, Warren and Bradford 2013), and standardized hand collecting is comparable to pitfall traps and baits in accumulating ant species (Gotelli et al. 2011).

### Spring phenology

A subset of 13 of the 35 sites (Supplementary Material S1) that represented the coastal-to-interior gradient (as we found that minimum temperatures were driven by lake rather than urban

gradients) were selected for 2017 ant spring phenology testing (April 3–May 12). At each site, three bait station points were established at least 100 m apart within wooded areas at each site. Three temperature dataloggers (HOBO U23 Pro v2; Onset, Bourne, MA) were buried 4 cm in the ground (to avoid diurnal temperature variance from sunlight, wind, etc.) at each bait station plot and programmed to sample temperature at 1200 and 2400 each day. We used small amounts of tuna (< 10 g) to provision bait stations (4 × 4 cm polystyrene weighing dishes secured into the soil with a 2-cm nail). Tuna contains chemical compounds similar to those in seed elaiosomes and dead insects (Marshall, Beattie and Bollenbacher 1979; Bestelmeyer et al. 2000). Hence, tuna baits attract scavenging ants, particularly early spring, seed-dispersing ants such as *Aphaenogaster* spp. (Ness, Morin and Giladi 2009; Warren, Giladi and Bradford 2014). Although tuna baits may limit nonscavenging ants from the phenology assessment, they have been shown to attract a considerable number of woodland ant species worldwide (Warren and Giladi 2014). All baits were provisioned weekly during the study period and monitored for 1 h to identify visitors.

### Data analysis

We used the means of each five-ant sample to calculate colony ( $CT_{min}$  and  $CT_{max}$ ). *Aphaenogaster picea* is very common in WNY, but a closely related congener, *A. rudis* (Enzmann, J., 1947), also occurs in the study region. *Aphaenogaster rudis* has been described as the ‘coastal’ *Aphaenogaster*, and it is more cold intolerant than *A. picea* in the southern end of its range (Crozier 1977; Warren and Chick 2013). For these reasons, we initially analyzed 28 *A. picea* colonies and 6 *A. rudis* colonies separately. However, we found no differentiation in *A. picea* and *rudis* in thermal tolerance using Student’s t-tests in the R statistical package (R Core Team Version 3.5.0 2016), so we compiled them for statistical analysis.

Given that Buffalo is located on the shore of Lake Erie, we checked for correlation between the lake and city gradients using Pearson’s correlation coefficient (R Core Team Version 3.5.0 2016) and found moderate correlation (0.57). For this reason, we then used Akaike’s Information Criterion (Akaike 1973) to select the best-fit model between distance from lake and distance from city ( $\Delta AIC > 2.0$ ) instead of putting both parameters in the same models. We tested the gradient influence on thermal tolerances using linear mixed models (LMM) with  $CT_{min}$ ,  $CT_{max}$  and  $CT_{range}$  ( $CT_{max} - CT_{min}$ ) as dependent variables and distances from lake and city as fixed effects in the *lme4* package (Bates et al. 2015). We used site as a random effect to account for autocorrelation as we collected multiple colonies in some sites.

We examined variation in the frequency of the nine most common ant species (by frequency > 30% of the sites; Supplementary Material S2) and the lake and city gradients with principal component analysis (PCA) using the *FactoMineR* and *factoextra* packages (Le, Josse and Husson 2008) in the ‘R’ statistical package (R Core Team 2017). We used the first 2 principal components, which explained 46% of the variance in loadings.

We examined ant species richness at the timed survey sites using generalized linear models (GLM) assuming quasi-Poisson distributed error (underdispersion < 1.0 in both models). Because the distance from lake and distance from city parameters similarly predicted ant richness ( $\Delta AIC < 2.0$ ), both models were retained.

We examined 2017 spring temperatures (April 3–May 12) using a LMM with climate zone (coastal and inland) and date (and a climate × day interaction term) as fixed effects. Because we clustered four bait stations at each of the 13 sites, we include site as a random effect to account for spatial autocorrelation.

We fit the mixed models using Analysis of Deviance (ANODEV) with Type II Wald chi-square tests. Given that some ant species recruit heavily to food resources (e.g. *Prenolepis imparis*) whereas others recruit few fellow foragers (e.g. *Aphaenogaster* spp.), we used the frequency of bait stations visits at each site (visits station<sup>-1</sup>) as the dependent variable rather than species abundance. We examined ant spring foraging frequency as a binomial proportion using a generalized linear mixed model (GLMM) with week and climate zone (and a week × climate zone interaction effect) as fixed effects. We included a site-level random effect and fit the GLMM with ANODEV.

## Results

### CT<sub>min</sub>, CT<sub>max</sub> and CT<sub>range</sub>

The two *Aphaenogaster* species had the same thermal tolerances (CT<sub>min</sub>:  $t = 0.432$ ,  $df = 12.669$ ,  $P\text{-value} = 0.672$ ; CT<sub>max</sub>:  $t = -1.447$ ,  $df = 7.857$ ,  $P\text{-value} = 0.286$ ). Distance to lake better predicted variation in *Aphaenogaster* CT<sub>min</sub> than distance to city ( $\Delta\text{AIC} = 3.4$ ). *Aphaenogaster* CT<sub>min</sub> increased with distance from lake (Coeff. = 0.031, SE = 0.013,  $t\text{-value} = 2.387$ ,  $P\text{-value} = 0.030$ ; Fig. 2A). For CT<sub>max</sub>, distance to city better predicted variation in *Aphaenogaster* thermal tolerance than did distance to lake ( $\Delta\text{AIC} = 3.7$ ). *Aphaenogaster* CT<sub>max</sub> decreased with distance from city (Coeff. = -0.012, SE = 0.004,  $t\text{-value} = -2.547$ ,  $P\text{-value} = 0.020$ ; Fig. 2B). For CT<sub>range</sub>, distance to lake better predicted *Aphaenogaster* variation than distance to city ( $\Delta\text{AIC} = 3.2$ ). *Aphaenogaster* CT<sub>range</sub> decreased with distance from lake (Coeff. = -0.036, SE = 0.013,  $t\text{-value} = -2.753$ ,  $P\text{-value} = 0.013$ ; Fig. 2C).

### Community responses

We found 34 ant species during timed surveys in 1400 min of times searches at 35 WNY parks (Supplementary Material S2). The most common ant genera were *Lasius* (five species), *Formica* (four species) and *Myrmica* (four species). The most common ant species were *L. alienus* (Foerster, 1850; found at 77% of the sites), *Camponotus pennsylvanicus* (De Geer, 1773; found at 63% of the sites) and *A. picea* (found at 57% of the sites).

Principal component analysis of the eight most frequent ant species and the lake and city gradients indicated most variation occurred along the PC1 axis (Fig. 3). The most important variables for PC1, based on percentage of contribution, were *A. picea* (21%) and *Lasius nearcticus* (Wheeler, W.M., 1906) [16%]. Distance from the city (16% contribution) and distance from the lake (16% contribution) appeared to weakly covary, and *A. picea* frequency covaried positively with greater distance from the city whereas *L. nearcticus* covaried positively with greater distance from the lake. The most important variables for PC2 were *C. pennsylvanicus* (25%), *F. subsericea* (Say, 1836) [23%] and *Lasius umbratus* (Nylander, 1846). *L. umbratus* covaried positively with distance from the lake (10% contribution), but *F. subsericea* and *C. pennsylvanicus* only covaried with one another.

Ant species richness in the timed survey sites increased with distance from the lake (Coeff. = 0.008, SE = 0.004,  $t\text{-value} = 2.060$ ,  $P\text{-value} = 0.047$ ; Fig. 4A) and with distance from the city (Coeff. = 0.008, SE = 0.004,  $t\text{-value} = 2.313$ ,  $P\text{-value} = 0.042$ ; Fig. 4B).

### Spring phenology

In spring 2017, a significant interaction term ( $\text{Chi} = 23.294$ ,  $df = 1$ ,  $P\text{-value} < 0.001$ ) indicated that inland temperatures were relatively cooler than coastal temperatures in early April, but by mid-May the pattern reversed, and inland temperatures were

relatively warmer (Fig. 5A). Mean ( $\pm$  SE) temperatures differed little between the coastal ( $9.8 \pm 0.1^\circ\text{C}$ ) and inland ( $10.1 \pm 0.1^\circ\text{C}$ ) sites during this period. Ants were much more frequent at coastal ( $25.0 \pm 4\%$ ) than inland ( $8.5 \pm 3\%$ ) baits during the spring period ( $\text{Chi} = 8.994$ ,  $df = 1$ ,  $P\text{-value} = 0.002$ ; Fig. 5B), and increased with week ( $\text{Chi} = 11.446$ ,  $df = 1$ ,  $P\text{-value} < 0.001$ ), but there was no significant climate zone × week interaction ( $\text{Chi} = 0.510$ ,  $df = 1$ ,  $P\text{-value} = 0.475$ ). The most common ant, based on bait station frequency, was *P. imparis* (53.3%), followed by *Myrmica rubra* (26.7%) and *A. picea* (10.0%).

## Discussion

We found considerable ant physiological, behavioral and community responses to seasonal coastal-to-interior climate inversions from the Great Lakes that generally overshadowed effects of the urban-to-rural gradient. *Aphaenogaster* ant thermal tolerance narrowed with greater distance from the lake, and physiological cold tolerance was lower nearer the lake. However, *Aphaenogaster* heat tolerance appeared better predicted by the urban center as it decreased with distance from the city. In 2017, historically low ice cover on the Great Lakes appeared to obliterate the coastal-to-interior spring temperature gradient, and coastal ant spring phenology was much earlier than inland ants, suggesting community-wide lower physiological cold tolerance. Moreover, woodland ant community richness increased with distance from both the lakes and the city, likely a combination of temperature and land-use gradients.

Greater variation in vertebrate and invertebrate thermal tolerances generally corresponds with greater variation in environmental temperatures (Janzen 1967), a pattern that holds true for ants (Warren and Chick 2013; Diamond et al. 2017b). Given that large water bodies moderate temperature extremes, we expected to find less cold and heat tolerance in ants nearer Lakes Erie and Ontario. Instead, we found greater cold tolerance nearer the lakes, and heat tolerance was better explained by proximity to the Buffalo urban center. Our error probably can be explained as an underappreciation of the complexities of 'lake effect'. Water and land have different heat capacities so that water imparts lagged atmospheric effects on leeward lands across seasons. In the autumn, warmer waters extend summer for proximate terrestrial landscapes and, in the spring, colder waters delay spring (Day 1832; Yocum 1913; Eichenlaub 1979). Fruit farmers long have taken advantage of these patterns to grow orchards in the thermal refuges at higher latitudes than the plants would otherwise reproduce (Yocum 1913). The delayed spring prevents the emergence of flower buds before the threat of frost has passed, and the extended autumn delays early frost. Reproductive cold stress is a trait that commonly limits crops as flower buds generally are more sensitive to cold than the plant itself (Rodrigo 2000; Zinn, Tunc-Ozdemir and Harper 2010; Salazar-Gutierrez et al. 2014). A similar pattern may impact ants near the lake. Given that we found ants near the lake to be more cold tolerant, these physiological and behavioral responses may reflect temperature impacts on spring brood development. Insect reproduction and mating success can be limited by extreme temperatures (Jones and Kunz 1998; Porcelli et al. 2017), and for ants in colder climates, spring is a critical point in their life history as colonies, or new queens, break dormancy and must initiate rapid brood development and food foraging for colony success. Hence, for those colonies nearer the lake, annual temperature may be less important than spring temperature, which may exert selection pressure toward greater cold tolerance.

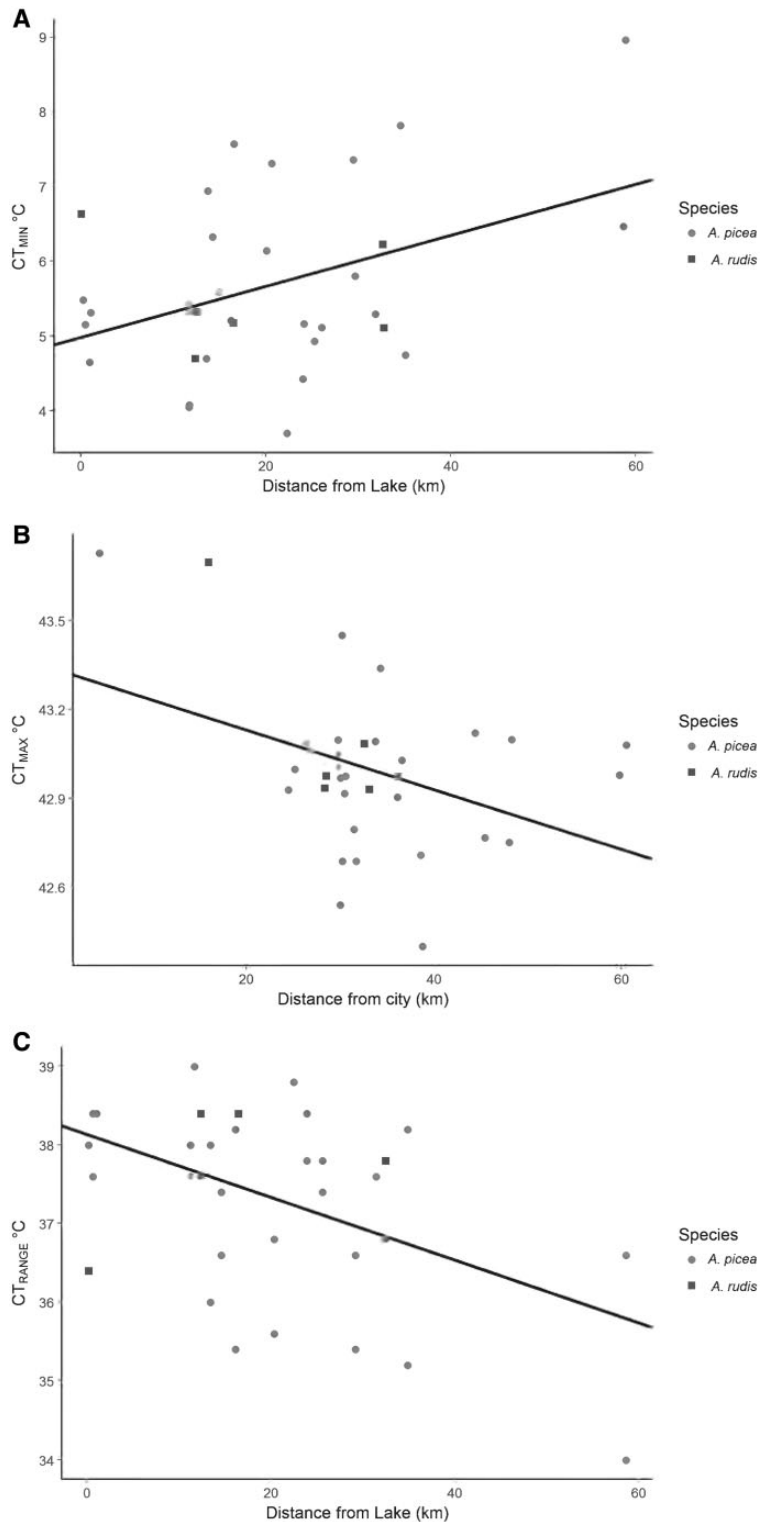


Figure 2: Regression plots showing *Aphaenogaster* spp. minimum cold tolerance ( $CT_{min}$ ) increased with distance from the Great Lakes (A: P-value = 0.017,  $R^2=0.16$ ); *Aphaenogaster* spp. maximum heat tolerance ( $CT_{max}$ ) decreased with distance from the Buffalo, NY (USA) city center (B: P-value = 0.020,  $R^2=0.16$ ) and *Aphaenogaster* spp. range of tolerance ( $CT_{range} = CT_{max} - CT_{min}$ ) decreased with distance from lake (C: P-value = 0.005,  $R^2=0.22$ )

Urbanization can increase local temperatures  $> 8\text{--}10^\circ\text{C}$  relative to proximate rural areas (Angilletta et al. 2007; Imhoff et al. 2010). As a result, urban ants often physiologically tolerate higher temperature than rural ants (Angilletta et al. 2007;

Diamond et al. 2017b). Even though urban areas are warmer than rural areas overall, urban temperature profiles generally are narrower than rural largely because higher night-time and winter temperatures contract the range (Imhoff et al. 2010).

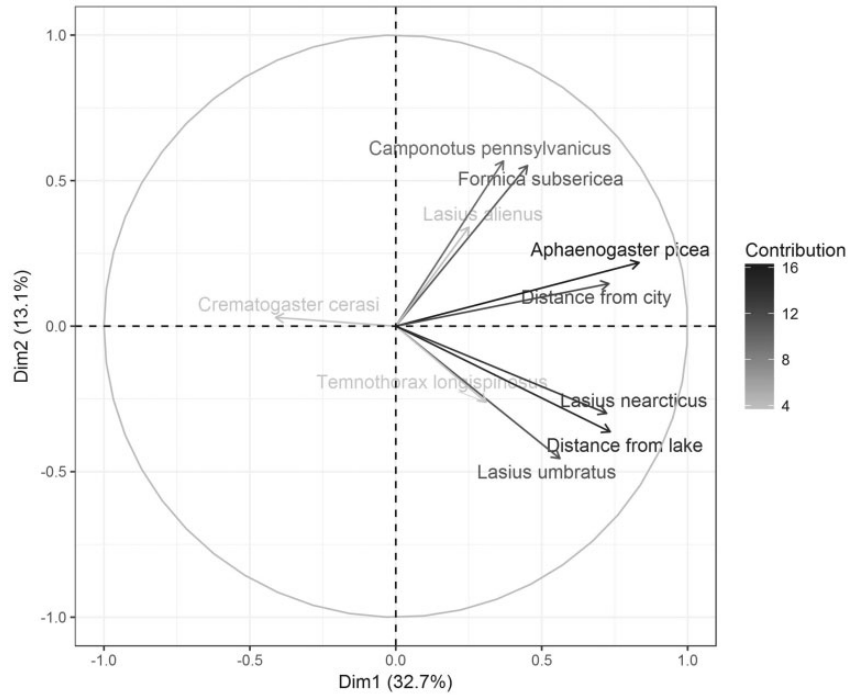


Figure 3: Principal component analysis of ant species frequency in WNY forest patches along with variables for distance from the Great Lakes and distance from the Buffalo, NY (USA) city center. Arrows pointing in the same direction indicate positive covariation and those pointing in opposite direction indicate negative covariation. Shading indicates percent contribution with darker shades indicating variables that contribute relatively more to the principal components axes

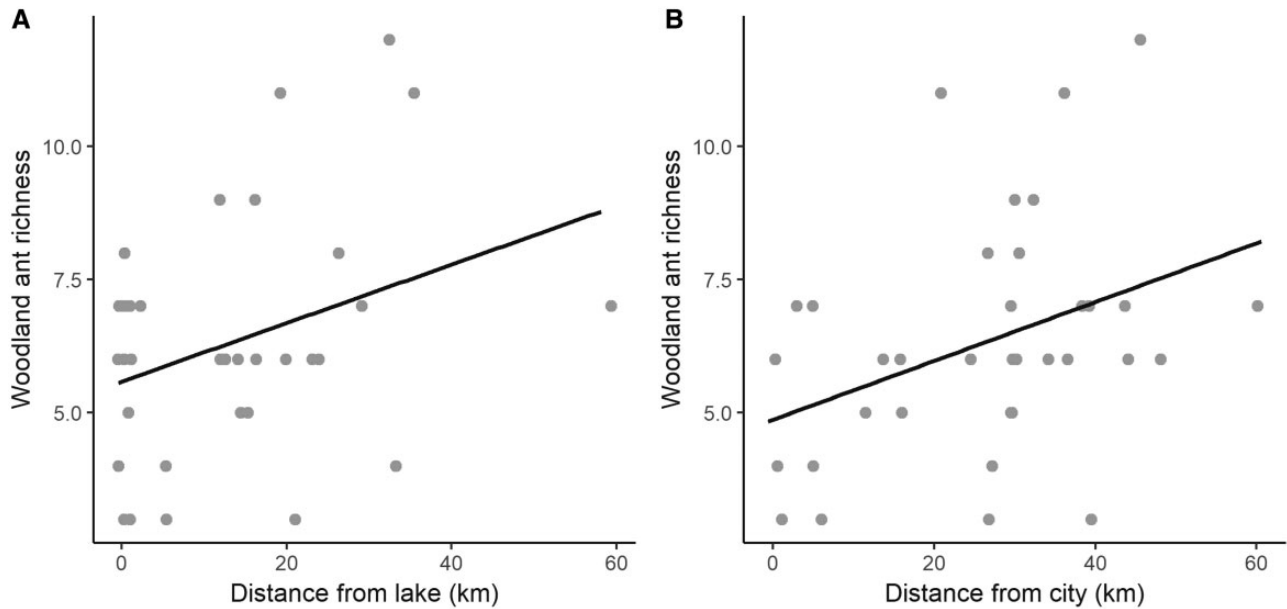
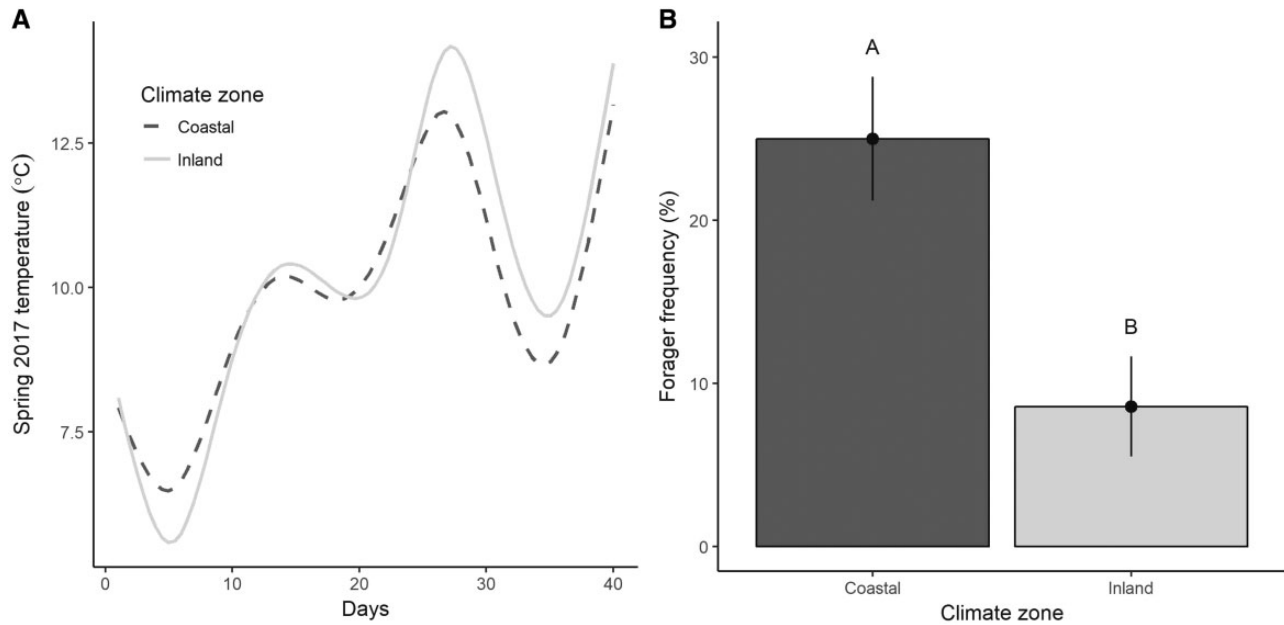


Figure 4: Regression plots showing ant species richness increases with distance from the Great Lakes (A:  $P$ -value = 0.047, pseudo- $R^2$  = 0.15), and distance from the Buffalo, NY (USA) city center (B:  $P$ -value = 0.027, pseudo- $R^2$  = 0.19)

Narrowed temperature tolerance in ants generally is explained by higher  $CT_{min}$  rather than lower  $CT_{max}$  (Wittman et al. 2010; Kaspari et al. 2015; Diamond et al. 2017b), which is the pattern we observed in *Aphaenogaster* with distance from the Great Lakes. However, along our urban-to-rural gradient, we found that *Aphaenogaster* ants had a lower  $CT_{max}$  but unchanged  $CT_{min}$ . Similarly, Angilletta et al. (2007) found that urban leaf cutter ants in São Paulo, Brazil had lower  $CT_{max}$  and unchanged

$CT_{min}$  relative to proximate rural areas. Conversely, Diamond et al. (2017b) found  $CT_{min}$  much higher in urban than rural ants and less change in  $CT_{max}$  in *Temnothorax curvispinosus* ants. Diamond et al. (2017b) conducted their studies in Cleveland, OH (USA), which is proximate to Lake Erie, as was our study area. One possibility for the discrepancy in studies may be an unmeasured lake effect, but we focused on *Aphaenogaster* species, which have lower heat tolerance than *T. curvispinosus*



**Figure 5:** Western New York spring soil temperature (April 3–May 12) during ant foraging phenology experiments (A). A significant interaction term ( $P$ -value  $< 0.001$ ) indicated that inland temperatures were relatively cooler than coastal temperatures in early April, but by mid-May the pattern reversed; however, the mean temperatures differed by  $< 0.3^{\circ}\text{C}$ . Spring foraging frequency was much higher at the coastal than inland sites in spring 2017 (B:  $P$ -value = 0.002). Spring foraging ants mostly included *P. imparis*, *M. rubra* and *A. picea*. Spring foraging frequency was calculated as the percentage of tuna bait stations at each study site visited by the ants during weekly 1-h observation trials. Tuna baits mimic dead insects and are a good indicator of the initiation of spring foraging by woodland ants as well as potential seed dispersers

(Penick et al. 2017) used by Diamond et al. (2017b). Still, the discrepancy suggests that further study is warranted into the interaction between the large-scale effects of water bodies and the mesoscale effects of proximate urbanization, as well as how urbanization and large-scale patterns combine to affect thermal tolerance in organisms.

Ant species richness generally increases with temperature (Dunn, Parker and Sanders 2007; Lessard et al. 2007), which suggests that WNY richness should be lowest with distance from the lake and city as the inland landscape has, on average, the lowest annual temperatures. We found the opposite, suggesting that, for woodland ants at our scale of measurement, land use may be more important than temperature for diversity. Ant species richness can be higher in urban than forested areas (Lessard and Buddle 2005); however, in general, North American ant species richness is higher in forested than proximate urban habitat (Uno, Cotton and Philpott 2010; Guénard, Cardinal-De Casas and Dunn 2015; Crist and Kaitlin 2017). We restricted our study sites to wooded patches, but the urban forest patches are smaller and more degraded than the rural forests (McKinney 2008; Olejniczak et al. 2018), which likely contributed to the diminished species richness. The increased frequency of some species was most impacted by greater distance from the city (e.g. *A. picea*), some species were most impacted by distance from the lake (e.g. *L. nearcticus* and *L. umbratus*) and some could be attributed to neither (e.g. *C. pennsylvanicus*, *F. subsericea*). *Aphaenogaster* spp. are relatively less thermophilic than other ant species (Penick et al. 2017), but they also are found only in woodlands (Lubertazzi 2012), which suggests that temperature and/or land use limited them near the urban areas. Little is known about the thermal tolerances of *L. nearcticus* and *L. umbratus*; both are found under rocks and stones in moist forests (Ellison et al. 2012). Given that we targeted woodland ant species readily found under downed wood and rocks, we may

have underestimated cryptic ant species, but there was no reason to assume an urban-to-rural bias in the sampling.

Coastal habitats near the Great Lakes generally stay colder longer in spring than inland habitats (Eichenlaub 1979; GLERL 2017). The lower thermal tolerances of coastal ants should offset that discrepancy so that coastal and inland ants initiate spring foraging at roughly the same time. However, a warm winter resulted in record low maximum ice coverage across the Great Lakes in 2016–2017 (36% lower than the long-term average and the fourth lowest since 1975, GLERL 2017). As such, verified by our temperature data, the usual spring temperature lag did not occur in spring 2017, making our phenology experiments essentially a common temperature garden experiment across coastal-to-interior ants. If ant species nearer the lake had lower  $CT_{\min}$ , as did the *Aphaenogaster* we measured, they should initiate spring foraging earlier in the common temperatures, which was observed. The most common ant species at the bait stations was *P. imparis*, known as the ‘winter ant’ because it is active during early spring and late autumn when other ants are dormant (Ellison et al. 2012). However, in WNY, *P. imparis* often is active throughout the summer, as we found it at 23% of our summer sampled sites. The second most common early ant was *M. rubra*, a nonnative ant that has invaded habitats along the lakeshore in WNY. Finally, the third most common early ant was *A. picea* (we found no *A. rudis* foraging in early spring).

Ant physiology, behavior and species sorted out along coastal-to-interior and urban-to-rural gradients. In some ways, the sorting was predictable, as urban ants tolerated higher temperatures than rural ants. In most ways, however, the results were contingent, with the influence of complex lake effects apparently interacting with ant life history and behavior in a conditional manner dependent on seasonal timing. Our data add to existing studies suggest that ant tolerance for minimum temperatures may be more important than high temperature



tolerance in determining fitness and, more so, community responses. Indeed, our results suggest that cold extremes may limit ants by interfering with spring reproduction, a testable hypothesis worth investigating. Our data also suggest that large-scale environmental gradients, here Great Lakes effect, may override, or at least complicate, mesoscale environmental gradients, here urbanization. In the end, our results suggest that winter cold extremes may select for cold-tolerant ants near the Great Lakes, whereas urbanization selects for ants with greater heat tolerance. These results suggest that the ability to detect and predict how species and communities will respond to warming temperatures may depend on a better understanding of how seasonal, versus annual, temperatures interact with key life history stages, as well as a better understanding of coastal-to-interior environmental gradients.

## Supplementary data

Supplementary data are available at JUECOL online.

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## Data accessibility

The data generated and analyzed for the current study are available in the SUNY Buffalo State Digital Commons [[https://digitalcommons.buffalostate.edu/biology\\_data/5/](https://digitalcommons.buffalostate.edu/biology_data/5/)].

## Conflict of interest statement

None declared.

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