Basal resistance enhances warming tolerance of alien over indigenous species across latitude

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Soil systems are being increasingly exposed to the interactive effects of biological invasions and climate change, with rising temperatures expected to benefit alien over indigenous species. We assessed this expectation for an important soil-dwelling group, the springtails, by determining whether alien species show broader thermal tolerance limits and greater tolerance to climate warming than their indigenous counterparts. We found that, from the tropics to the sub-Antarctic, alien species have the broadest thermal tolerances and greatest tolerance to environmental warming. Both groups of species show little phenotypic plasticity or potential for evolutionary change in tolerance to high temperature. These traits differences between alien and indigenous species suggest that biological invasions will exacerbate the impacts of climate change on soil systems, with profound implications for terrestrial ecosystem functioning.

The impacts of climate change and biological invasions continue to increase in magnitude (1, 2), yet investigation of their interactions remains fragmented and incomplete (3). The general expectation is that such interactions will benefit alien over indigenous species, and thus have negative consequences for native biodiversity (4). Soil systems are globally important reservoirs of biodiversity, influence aboveground ecological dynamics, and are critical for food security (5). They are also highly susceptible to climate change and to biological invasions, which both have major effects on soil ecosystem functioning and are expected to interact to the detriment of these systems (6, 7). Understanding how climate change–invasion interactions will play out in soil systems is, therefore, pressing (8). For the soil biota, increasing temperature is one of the most significant components of climate change (9). Differential fitness effects of rising temperatures on indigenous compared with alien species must necessarily be mediated by consistent thermal trait differences between these two groups of species (10). Moreover, if such effects are general, these trait differences between alien and indigenous species should be maintained across a broad latitudinal— and hence climatic—range. No study has yet evaluated whether alien species have broader thermal tolerance limits and greater tolerance to climate warming than their indigenous counterparts.

To assess this expectation, we investigated the thermal limits to activity in 16 alien and 14 indigenous species of springtails (Collemboala) spanning a climatic gradient from the Australian tropics (16°S) to south of the Antarctic Polar Front (54°S) (Fig. 1). Springtails are globally distributed, functionally significant component of the soil biota (5, 11). The group includes many alien species that have invaded soil systems from the polar regions to the tropics (6, 12). Critical thermal limits to activity form a useful proxy for adult fitness because organisms are incapable of movement outside of these limits, thus reducing fitness (13, 14), with demographic effects reflected in associations between critical thermal limits and geographic ranges in several taxa (15, 16). Upper critical thermal limits are also now widely used to assess tolerance to climate change–associated warming in a wide range of organisms (17, 18). Using a single consistent method [in contrast with multiple methods represented in and which complicate interpretations of meta-analyses (19)], the F2 generation of populations of each species to overcome parental effects and the potential for laboratory adaptation (20), and taking account of the influence of phylogenetic relatedness (21), we investigated both basal thermal tolerance and the extent of phenotypic plasticity in the upper critical thermal limits. Although phenotypic plasticity of thermal tolerance traits may only play a limited role in reducing exposure to climate change in some ectotherms (22), it has been identified as a potentially significant mediator of responses to thermal challenge (23), including in springtails (9, 24). Phenotypic plasticity is also thought to be a major contributor to the success of invasive species (25, 26). In addition, total thermal tolerance range and lower critical thermal limits play a role in determining range shifts in response to environmental change (16). Thus, we not only assessed basal tolerance, but also phenotypic plasticity for both upper and lower critical thermal limits. We evaluated whether climate-related variation in upper and lower critical thermal limits, thermal tolerance range, and warming tolerance— the difference between species’ upper critical thermal limits and maximum environmental temperatures (17)—differ systematically between the indigenous and alien springtail species. Tests were conducted using phylogenetic generalized least squares (PGLS) (21), and a phylogenetic tree constructed from molecular markers to take into account phylogenetic signal in the traits measured. Evolutionary responses have the potential to reduce substantially the impacts of climate change on populations (27, 28). Therefore, we also examined the extent to which thermal traits might evolve in springtails and whether this potential differs between indigenous and alien species. We used laboratory natural selection (29) to assess the extent of evolutionary potential in the critical thermal limits.
of an indigenous and alien species from the tropics and another such pair of species from the temperate zone, held at elevated temperatures just below those that substantially depress fitness in these species, so reflecting extreme environmental conditions.

**Results**

**Critical Limits and Warming Tolerance.** Although critical thermal maximum \((CT_{\text{max}})\) increased by \(0.16 \pm 0.07 \degree C\) (mean \(\pm SE)\) on average for each \(1 \degree C\) increase in soil microhabitat temperature \([\text{obtained from MODIS Land surface temperatures (Materials and Methods)}]\) across latitude, the indigenous species had, on average, a \(2.9 \pm 0.8 \degree C\) lower \(CT_{\text{max}}\) than their alien counterparts (Fig. 2A), with little evidence of phylogenetic signal in the trait (Table 1). For critical thermal minimum \((CT_{\text{min}})\), the magnitude of change with microhabitat temperature variation was similar (Fig. 2B) \((0.18 \pm 0.08 \degree C\) increase per \(1 \degree C\) change in microhabitat temperature). The difference between the two groups was, however, smaller \((0.5 \pm 0.9 \degree C)\), with an important contribution of phylogenetic relatedness to trait variation, which rendered the difference between the indigenous and alien species nonsignificant (Table 1). Although \(CT_{\text{max}}\) and \(CT_{\text{min}}\) were not significantly related \([\text{SI Appendix, Fig. S1 and Table S1)}]\), similar covariation of each of these variables with microhabitat temperature meant that tolerance range showed no association with microhabitat temperature. Nonetheless, a large difference in tolerance range, of on average \(3.4 \pm 1.1 \degree C\) (Fig. 2C), was found between the indigenous and alien species, with strong phylogenetic signal in the trait (Table 1). Thus, overall, upper and lower critical temperatures varied in similar ways with microhabitat temperature across latitude, resulting in no microhabitat-associated variation in thermal tolerance range. Consistently large differences among the indigenous and alien species were, however, found in \(CT_{\text{max}}\) and tolerance range. Warming tolerance declined by \(1.1 \pm 0.08 \degree C\) with every \(1 \degree C\) increase in soil microhabitat temperature across latitude for both groups, but the alien species had, on average, a \(2.8 \pm 0.8 \degree C\) larger warming tolerance than the indigenous species (Fig. 2D), with no trait variation accounted for by phylogenetic relatedness (Table 1). Alien species were, therefore, on average more tolerant of warming across latitude than their indigenous counterparts.

**Evolutionary Potential and Phenotypic Plasticity.** Across the four species examined for evolutionary responses to elevated temperatures, \(CT_{\text{max}}\) showed little evolutionary response over 10–18 generations. Although the treatments were significant in three of the four species \([\text{SI Appendix, Table S2)}]\), observed responses to selection per generation across all species were small, ranging from 0 to \(0.89 \degree C\) (Fig. 3 and \textit{SI Appendix, Table S3)}], with a maximum overall response of \(0.6 \degree C\) in the selected lines of the alien
temperate Orthonychiurus sp. Moreover, the responses in $\text{CT}_{\text{max}}$ remained within the scope of developmental phenotypic plasticity for all four species (Fig. 3 and SI Appendix, Table S4), accounting for the smaller than expected observed responses of $\text{CT}_{\text{max}}$ to selection (SI Appendix, Table S3). These changes in $\text{CT}_{\text{max}}$ for the four species were much more limited than those of $\text{CT}_{\text{min}}$, which showed larger intergenerational changes, and typically larger than those achievable through developmental plasticity (SI Appendix, Figs. S2 and Tables S5 and S6).

Although acclimation responses varied substantially among the traits and species (Fig. 1), acclimation response ratio (ARR), a measure of phenotypic plasticity (22), showed no systematic difference between the indigenous and alien species for either $\text{CT}_{\text{max}}$ or $\text{CT}_{\text{min}}$ (SI Appendix, Table S7), resulting in no influence on warming tolerances either. Overall, $\text{CT}_{\text{min}}$ typically showed greater phenotypic plasticity (ARR mean: 0.137, range: 0.037–0.238) than $\text{CT}_{\text{max}}$ (ARR mean: 0.047, range: 0.008–0.109) [ANOVA $F_{(1,58)} = 64.05, P < 0.0001$], but no variation in ARR was found with microhabitat temperature or with basal tolerance in either trait (SI Appendix, Table S7). Theory suggests that broader performance curves in temperate species relative to tropical species might differentially influence responses to acclimation exposures of similar magnitudes (17), but such differences were not detected.

**Discussion**

In plants and in some animal groups, indigenous and alien species frequently differ systematically either in basal trait values or, over the short-term, in phenotypic plasticity, which may account, at least in part, for the success of alien species (25, 26, 30, 31). Only a few studies have also sought to interpret these differences in a climate change context and typically just for specific locations (10, 32, 33). Hence, evidence that climate change may favor alien species over their indigenous counterparts via differences in trait values is limited (3).

**Table 1. Outcome of PGLS analyses**

| Trait | Estimate (SE) | T | P |
|-------|--------------|---|---|
| **CT values and warming tolerance ranges** | | | |
| Intercept | 35.79 (1.37) | 26.13 | <0.001 |
| Median soil temperature | 0.16 (0.07) | 2.25 | 0.033 |
| Status (indigenous) | -2.93 (0.81) | -3.62 | 0.001 |
| $F_{(2,27)} = 8.46, P = 0.001, R^2 = 0.34, ML_{\lambda} = 0.00$ |
| **CT_{min}** | | | |
| Intercept | -4.10 (1.90) | -2.15 | 0.040 |
| Median soil temperature | 0.18 (0.08) | 2.32 | 0.028 |
| Status (indigenous) | 0.54 (0.94) | 0.57 | 0.571 |
| $F_{(2,27)} = 2.76, P = 0.081, R^2 = 0.11, ML_{\lambda} = 0.44$ |
| **Tolerance range** | | | |
| Intercept | 39.57 (2.38) | 16.66 | <0.001 |
| Median soil temperature | -0.006 (0.096) | -0.07 | 0.947 |
| Status (indigenous) | -3.35 (1.14) | -2.95 | 0.007 |
| $F_{(2,27)} = 4.39, P = 0.022, R^2 = 0.19, ML_{\lambda} = 0.49$ |
| **Warming tolerance** | | | |
| Intercept | 42.83 (2.30) | 18.62 | <0.001 |
| Maximum soil temperature | -1.08 (0.08) | -13.98 | <0.001 |
| Status (indigenous) | -2.82 (0.79) | -3.57 | 0.001 |
| $F_{(2,27)} = 101, P < 0.001, R^2 = 0.87, ML_{\lambda} = 0.00$ |

**Outcome of PGLS analyses showing change in thermal tolerance ($^\circ$C) with median (or maximum for warming tolerance) daytime soil surface temperature ($^\circ$C) and the difference among indigenous and alien species. ML$\lambda$ is the maximum-likelihood estimate of Pagel's $\lambda$ (21), a measure of phylogenetic effect where 0 indicates no effect and 1 indicates a strong effect equivalent to that expected under a BM model of evolutionary change.**
evolutionary change in \( CT_{\text{max}} \) in the springtail species assessed (and in contrast to substantial phenotypic plasticity and potential for evolutionary change in \( CT_{\text{max}} \)) are in keeping with what has been found for other animal groups (22, 34). They indicate that thermal tolerance differences between the indigenous and alien groups are likely to persist through time. Nonetheless, thermal conditions different to those adopted in the laboratory selection experiment, such as occasional extreme events (39), might be more effective in driving evolutionary change in \( CT_{\text{max}} \) (28). Indeed, past evolutionary responses to divergent thermal conditions, in conjunction with the ecological conditions that promote the success of alien species (7), may explain the observed trait differences between the two groups of species in the first place. Such a mechanistic macro-physiology of biological invasion remains to be developed.

Given that trait differences between the alien and indigenous groups will likely endure, springtail assemblages should, with ongoing climate change, be more prone to dominance by alien species, irrespective of whether these assemblages are tropical, temperate, or more polar. Indeed, evidence from some areas suggests that such a process is already underway (6, 12, 32). Clearly, interspecific variation exists in thermal traits and warming tolerance among the springtail species investigated here (Fig. 1), and other life-history traits might also play a role (15), suggesting that specific predictions may be complicated. Nonetheless, the general trends we demonstrate support growing concerns that soil systems will be significantly impacted by interactions among climate change and biological invasion (7, 8).

The broader influence of such climate change–invasion interactions is likely to be realized through changes to soil-system dynamics. Springtails are widely known to have considerable effects on soil-system functioning, which can result in aboveground changes to system properties and functioning, influencing higher trophic levels (40, 41). For example, soil-dwelling springtails alter aboveground plant biomass and either lower or increase herbivore reproduction depending on the specific host plant (42). Moreover, these effects differ substantially between different springtail species, and influence belowground faunal interactions, such as between earthworms and springtails, again affecting the aboveground component of systems (11, 42). These findings, widespread invasion of soil systems by springtails (6), warming-related dominance of springtail assemblages (12), and different functional effects between alien and indigenous springtail species (43), indicate that interactions between warming and soil invasions will result in substantial changes to system functioning. Thus, differential success of alien over indigenous species as climates change is likely not only to have an effect on soil biodiversity and belowground ecological functioning, but also on aboveground ecosystems. In consequence, our work suggests that biological invasions stand to increase substantially the already pronounced impacts of climate change on terrestrial ecosystems across the planet.

Materials and Methods

Extended protocol descriptions are provided in the SI Appendix.

Collection, Identification, and Alien Species Assignment. The 30 springtail species were collected typically from across Australia (SI Appendix, Table S8) between 2013 and 2016. The focus was on hemiedaphic (litter-dwelling) species. Individuals were initially assigned to species in the field and at least 200 individuals collected per species. Collections were returned to the laboratory typically within 1 wk of collection. Species were identified to genus, and where species had been described, to species level using available keys (e.g., refs. 44 and 45). DNA barcoding was used to confirm species identifications. Mitochondrial DNA extraction and sequencing of the cytochrome c oxidase subunit I gene was undertaken by the Biodiversity Institute of Ontario, University of Guelph, Canada, following standard protocols developed for springtails (46). Sequences of 74 specimens from 23 species were compared with the >75,000 springtail sequences available through the Barcode of Life Data Systems (BOLD: www.barcodinglife.org) (SI Appendix, Table S9). Individuals that could not be identified using available keys and which were not represented in BOLD were examined by one of the authors (C.J.-S.), in discussion with other systematic experts, and assigned to uniquely identifiable species based on morphological characteristics or a barcoding gap of at least 2.5% (47). Sequences are available on BOLD (www.boldsystems.org) as part of Project COLMU (Colembola of Monash University). Species that were clearly identified as indigenous to Australia or to the sub-Antarctic islands in faunal treatments and those similarly identified as alien to either of these regions were retained as such in the classification of species as alien or indigenous. Undescribed species not represented in BOLD previously, or represented only from individuals already collected across Australia, New Zealand, or south of the Wallace line were considered indigenous. Following previous authors (6), undescribed species that had sequences present in BOLD from other distant tropical regions (such as the Neotropics) or from the Holarctic (typically Europe) were considered alien species (SI Appendix, Tables S8 and S9). Given the extensive nature of the BOLD information on springtails (>75,000 sequences, representing several thousand species), and the systematic expertise we consulted, we have high confidence in the species assignments to alien or indigenous species.

Site Microclimate Characteristics. The soil microclimate characteristics of each site were calculated using remote-sensed daytime land-surface temperature data from the MODIS satellite network (MOD11C2 v006; 30 arcsecond spatial resolution); 8-d temporal resolution from January 2001 to December 2015; doi:10.5067/MODIS/MOD11C2.006), which were linearly transformed to account for the diffusion of heat from the land surface to 2.5 cm below the soil surface. The slope of this linear
transformation was derived from the microclim dataset (48), which contains validated estimates of soil temperature for each hour in a 24-h cycle of an average year in each of the average year conditions. The median (MODIS soil median), 99% quantile (MODIS soil99), and maximum soil temperature (MODIS soil max; i.e., the warmest 8-d mean) of each site were calculated from our linearly transformed MODIS time series.

Colonial Colony Maintenance. Species were reared at constant rearing temperatures that typically reflect the average soil temperatures of the sites at which they were collected (SI Appendix, Table S8) in controlled-temperature incubators (MIR-154; SANYO Electric) on a 12-h light:12-h dark light cycle. Incubator temperatures were monitored using Hygrochron iButtons (DS 1923-F5; Maxim Integrated) (SI Appendix, Table S8). The F2 generation was the focus of this work (SI Appendix, Fig. S4) to minimize any carryover effects from the environment of origin, including parental effects, and to reduce the possibility of adaptation to laboratory conditions (29). Between 50 and 200 adults from the collected (F0) individuals were randomly assigned to two to four 60-mL pots lined with moistened Plaster-of-Paris: Charcoal powder (9:1) substrates. De-ionized water was added once to twice a week to maintain high humidity and, depending on the species, individuals were fed two to three times a week with algae from the bank of Platanus sp. or on slime mold ad libitum (49), enabling individuals to select nutrients optimally. Adults from the F2 generation (average egg to adult development time among the species is 74.16 ± 2.40.56 (SD)) were used for most experiments (SI Appendix, Fig. S4).

Accclination to Assess Phenotypic Plasticity. Before the experimental trials, all species were subject to temperature treatments (referred to as “acclimation” hereafter), undertaken in controlled-temperature incubators (MIR-154; SANYO), with temperatures verified using Hygrochron iButtons and under 12-h light:12-h dark conditions (SI Appendix, Table S8). Acclimation treatments lasted 7 d, given that complete responses usually occur within less time in terrestrial arthropods (30). Low, medium, and high acclimation temperatures were set at 5 °C below and 5 and 10 °C above standard rearing temperatures, respectively (SI Appendix, Fig. S4). For control temperatures, individuals were subject to the same manipulation as those in the acclimation treatments.

Critical Thermal Limit and Warming Tolerance Determinations. Critical thermal limits (CTmax and CTmin) were determined following standard methods (24, 51). All analyses were conducted in R v3.3.1 (56). PGLS (57), as implemented in the caper v0.52.0 (58) and APE (59) packages, was used to investigate relationships between species mean critical thermal limits (either CTmin, CTmax, or environment median). Approximately 45 individuals were assessed per replicate, line per treatment at each sampling period. The degree of plasticity associated with any phenotypic changes observed during the selection experiment was assessed using a reciprocal transplant experiment, investigating developmental plasticity. This involved switching individuals from the selection conditions to the control conditions and vice versa. Individuals were switched within 1 d of generation four for the temperate species and generation six for the tropical species. These different generations were used because of the slower development time of the temperate species. Thermal limits were assessed when the switched individuals had reached adulthood.

Statistical Analyses. All analyses were conducted in R v3.3.1 (56). PGLS (57), as implemented in the caper v0.52.0 (58) and APE (59) packages, was used to investigate relationships between species mean critical thermal limits (either CTmin, CTmax, or environment median). Differences were assessed using a Student’s t test or a Mann-Whitney U test, as appropriate. Species mean critical thermal limits were analyzed using linear mixed-effects models (LMMs) with species status (alien or indigenous), springtail species mean mass, and species status (alien or indigenous). A phylogeny for the species was constructed based on joint considerations of two recent molecular phylogenies for the group (60, 61), with species relative positions based on the cytochrome c oxidase subunit I gene phylogeny, or in a few cases on morphological similarity adjudicated by one of us (C.J.-S.). The barcoding placements were obtained from a neighbor-joining tree using standard methods. For the final tree, branch lengths were pruned as required to achieve a maximum likelihood value of each species (SI Appendix, Fig. S5). The data were available as a Newick file. Initially, two covariance matrices were constructed following either Brownian motion (BM) or Ornstein–Uhlenbeck (OU) models of evolution (63). Akaike Information Criterion values of BM and OU models were compared to identify which model of evolution provided the best fit to observed data using the APE (59) and nlme v3.1-131 (64) packages. Phylogenetically corrected models based on BM covariance matrices were a consistently better fit than those based on other evolutionary assumptions (SI Appendix, Table S11), thus the outcomes of these models are reported primarily, although for comparative purposes we provide the OU outcomes as well (SI Appendix, Table S12). For the BM models, a maximum-likelihood approach provided Pagel’s z (21) to indicate the degree of phylogenetic correlation in the data. The PGLS approach was used to investigate relationships between warming tolerance and environmental conditions (MODIS soil median), species mass, and species status, and to investigate relationships between CTmin and CTmax. Analyses were repeated using ordinary least-squares approaches as implemented in the linear model function of R v3.3.1, and coefficients were typically similar to those found in the PGLS models (SI Appendix, Table S13). Throughout, mass did not appear as a significant term in the models, and in no cases did slopes of the relationships between critical thermal limit traits and environmental features differ between the alien and indigenous species groups. For investigations of the ARR and its relationship with mean trait values, ordinary least-squares methods indicated no significant relationships and PGLS bore out these conclusions.

For the selection experiment, to analyze differences in critical thermal limits between selection and control lines, nested mixed-effect model analyses were conducted using the lmer function in the lme4 package (v1.1-13) (65) in R (v3.3.1). “Treatment” (control or selection) and “generation number” were treated as fixed effects, and “replicate line” was nested within treatment as a random effect (66). Nested mixed-effects analyses were also undertaken to analyze data from the reciprocal transplant experiment examining developmental plasticity. This involved comparing the critical thermal limits of the selection, control, and reciprocally transplanted lines at the respective generation of the reciprocal transplant experiment, with “replicate line” nested within treatment (control, selected, reciprocally transplanted) as a random effect. Separate analyses were performed for each of the four species.
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