



It is hot and cold here: the role of thermotolerance in the ability of spiders to colonize tree plantations in the southern Atlantic Forest

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Received: 19 September 2023 / Accepted: 14 February 2024 / Published online: 2 April 2024
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Abstract

Worldwide, with the decline of natural habitats, species with reduced niche breadth (specialists) are at greater risk of extinction as they cannot colonise or persist in disturbed habitat types. However, the role of thermal tolerance as a critical trait in understanding changes in species diversity in disturbed habitats, e.g., due to forest replacement by tree plantations, is still understudied. To examine the role of thermal tolerance on the responses of specialist and generalist species to habitat disturbances, we measured and compared local temperature throughout the year and thermotolerance traits [upper (CTmax) and lower (CTmin) thermal limits] of the most abundant species of spiders from different guilds inhabiting pine tree plantations and native Atlantic Forests in South America. Following the thermal adaptation hypothesis, we predicted that generalist species would show a wider thermal tolerance range (i.e., lower CTmin and higher CTmax) than forest specialist species. As expected, generalist species showed significantly higher CTmax and lower CTmin values than specialist species with wider thermal tolerance ranges than forest specialist species. These differences are more marked in orb weavers than in aerial hunter spiders. Our study supports the specialisation disturbance and thermal hypotheses. It highlights that habitat-specialist species are more vulnerable to environmental changes associated with vegetation structure and microclimatic conditions. Moreover, thermal tolerance is a key response trait to explain the Atlantic Forest spider's ability (or inability) to colonise and persist in human-productive land uses.

Keywords Arachnics · Ectotherms · Generalists · Niche breadth · Specialists

Communicated by Stefan Scheu.

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Introduction

The main stressors underlying species decline are land-use change, climate change, agriculture, introduced species, nitrification, and pollution (Wagner et al. 2021). Anthropogenic disturbance of natural ecosystems reduces species richness and changes species composition in biological communities (Ernst and Rödel 2005; Dolný et al. 2021). However, native species respond differently to habitat disturbance depending on their ecological and physiological requirements and their dispersion capacities (Tuomainen and Candolin 2011). Within a community, the niche breadth ranges from species highly dependent on specific resources and microhabitat conditions (habitat specialists) to a few species with the ability to exploit diverse resources and tolerate a broader range of environmental conditions (habitat generalists) (Levins 1968; Pandit et al. 2009; Devictor et al. 2010). The specialisation-disturbance hypothesis states that disturbances affect specialist species more due to their specific niche requirements (Vázquez and Simberloff 2002;

Wilson et al. 2008). Consequently, with the decline of natural habitats worldwide, species with reduced niche breadth are at increased risk of extinction as they cannot persist in or colonise disturbed habitats (Chichorro et al. 2022). In contrast, species with a wider niche breadth can persist in or even increase abundance in disturbed habitats (Brown 1984; Marvier et al. 2004).

Among the multiple dimensions of the ecological niche, thermal tolerance is a key factor explaining the presence and abundance of species in a particular habitat (Angilletta 2009; de Bello et al. 2021). Depending on their magnitude, value, and duration, thermal fluctuations affect survival of organisms. Whereas both endotherms and ectotherms are affected by thermal fluctuations, and extreme conditions can induce the mortality of individuals (McKechnie and Wolf 2019), ectotherms are more susceptible to thermal fluctuation, as their body temperature is coupled to the ambient temperature, meaning that they are highly dependent on environmental conditions to regulate body temperature, which affects life history traits and performance (Huey and Kingsolver 1989; Angilletta et al. 2002; Paaajmans et al. 2013; Rolandi and Schilman 2018). Recent studies on ectotherms showed that forest specialists exhibit lower thermal tolerance compared to generalist species (Nowakowski et al. 2017; Barahona-Segovia et al. 2019, 2022; Woon et al. 2022). However, there is a common trend among terrestrial ectotherms showing lower variation in upper than lower thermal limits (Araújo et al. 2013).

In forest ecosystems, the canopy of trees reduces solar radiation, maintaining stable temperature and humidity conditions in the understory (Kovács et al. 2017). Furthermore, the spatial heterogeneity of forests, due to the complexity of vegetation and vertical stratification, provides thermal refugia or shelters for organisms (Monasterio et al. 2009; Kaspari et al. 2015). Stable conditions and thermal refuges are essential in seasonal ecosystems where fluctuations in temperature and humidity can occur throughout the year (Barahona-Segovia et al. 2022). In contrast, intensive human land use drastically changes and homogenizes resources and conditions, mainly by completely replacing native vegetation diversity and structure (Barahona-Segovia et al. 2022). Due to these changes, only a small proportion of forest species can persist in human land uses in tropical and subtropical forests, partially due to their limited thermal tolerance (Díaz et al. 2013; Filgueiras et al. 2015; Costa et al. 2021). However, functional traits (such as thermal tolerance) that allow species to persist in human-disturbed habitats are only beginning to be understood.

Climate change is an important threat to spiders, among many anthropogenic threats (land-use change, agriculture, invasive species, nitrification and pollution) that may have an additive or synergistic effect on species decline (Wagner et al. 2021; Harvey et al. 2023). As ectotherm organisms, spiders

are an excellent model of study to explore the role of thermal tolerance on the capacity of species to persist or recolonise disturbed habitats (Humphreys 1987; Stevenson 1985). They are among the most diverse arthropod groups and have colonised most terrestrial environments, including anthropogenic landscapes (Jocqué and Dippenaar-Schoeman 2006; Benamú et al. 2017), where they provide essential ecological functions such as regulating arthropod populations (Prieto-Benítez and Méndez 2011; Nyffeler and Birkhofer 2017). In addition, spiders are an essential element of food webs for small mammals, birds, reptiles, and other arthropods (Foelix 2011). Spiders deal with thermal fluctuating conditions through behavioural strategies (e.g., refuge building, web relocation, and orientation), morphological features such as colouration or structural characteristics, and physiological response traits (i.e., cuticle wax composition associated with the prevention of water loss and thermal tolerance resistance) (Riechert 1976; Cloudsley-Thompson 1983; Rao and Mendoza-Cuenca 2016; Malmos et al. 2021). However, the role of thermal tolerance in spiders as a mechanism to explain changes in local community composition after anthropogenic disturbance of natural habitats has not been explored.

The southern Atlantic Forest is one of the most threatened ecosystems worldwide (Myers et al. 2000). Previous studies in this ecosystem have evaluated changes in species diversity due to forest replacement by pine plantations in several arthropod taxa, including beetles, ants, and spiders (Pacheco and Vasconcelos 2012; Fonseca et al. 2009; Gómez-Cifuentes et al. 2017). For spiders, Munévar et al. (2018, 2022) found a drastic decrease in species and trait richness when comparing native forest and pine plantations of different ages. However, the physiological mechanisms behind these changes are unknown.

Here, we investigate the role of thermal tolerance as a critical trait to understand the observed changes in spider diversity due to forest replacement by tree plantations and thus understand how some species could colonise and persist in this land use. For this purpose, we compared thermotolerance traits such as the critical thermal maxima (CT_{max}) and minimum (CT_{min}) of spiders from different species and guilds, inhabiting both pine plantations and native forests (generalists) or restricted to native forests (specialists). Following the thermal adaptation hypothesis (Angilletta, 2009), we expected generalist species to have a wider thermal tolerance range (lower CT_{min} and higher CT_{max}) than forest specialists.

Methods

Study area

We conducted the study in the semideciduous Atlantic Forest of north-eastern Argentina (Fig. 1). The mean annual

precipitation reaches 2000 mm without a dry season, and the mean annual temperature is 20 °C, with defined cold and hot seasons (Oliveira-Filho and Fontes 2000). We collected spiders from October to November 2021 and August 2022 in two contrasting habitats: young *Pinus taeda* plantations (1–2 years) and native forest. We selected three sites within each habitat separated by a minimum distance of 500 m. Young pine plantations have an extremely simplified vegetation structure and composition, bare soil, lower humidity values, and higher daily and seasonal thermal fluctuations compared to native forests (Peyras et al. 2013; Munévar et al. 2018; Santoandré et al. 2021) (Fig. 1). On the contrary, the native forest has trees between 20 and 40 m in height, with at least three different strata, and a dense understory of bamboo or arborescent ferns (Galindo-Leal et al. 2003) (Fig. 1).

Field microclimatic conditions

To describe the microclimatic conditions in young pine plantations and native forests, we recorded temperatures every 10 min throughout the year at six sites of native forests and pine plantations, using HOBO U23 Pro v2 External Temperature/Relative Humidity Data Logger. Part Number U23-002A (Onset Computer Corporation, Bourne, MA,

USA). We calculated the average daily maximum, minimum and the thermal amplitude range from these data. We have placed the dataloggers at ground level in a shaded location within each site to avoid direct sunlight. We choose sites representative of each type of environment. Operating range: External temperature sensor: – 40 to 70 °C (– 40 to 158 °F). Accuracy: ± 0.25 °C from – 40 to 0 °C (± 0.45 from – 40 to 32 °F), ± 0.2 °C from 0 to 70 °C (± 0.36 from 32 to 158 °F); Resolution: 0.04 °C (0.072 °F). Response time (typical to 90%): external temperature sensor: 3 min, 45 s in air moving at 1 m/s.

Species selection, collection and functional characterisation

First, we identified the most abundant species inhabiting young plantations and native forests (habitat generalists) and those restricted to native forests (habitat specialists), based on a previous study conducted in the same study area (Munévar et al. 2018). This study provides a database of spider species abundance systematically sampled over two years in five sites of young pine plantations and five sites of adjacent native forest, so we have prior knowledge of the community. The plantations are located within a matrix of

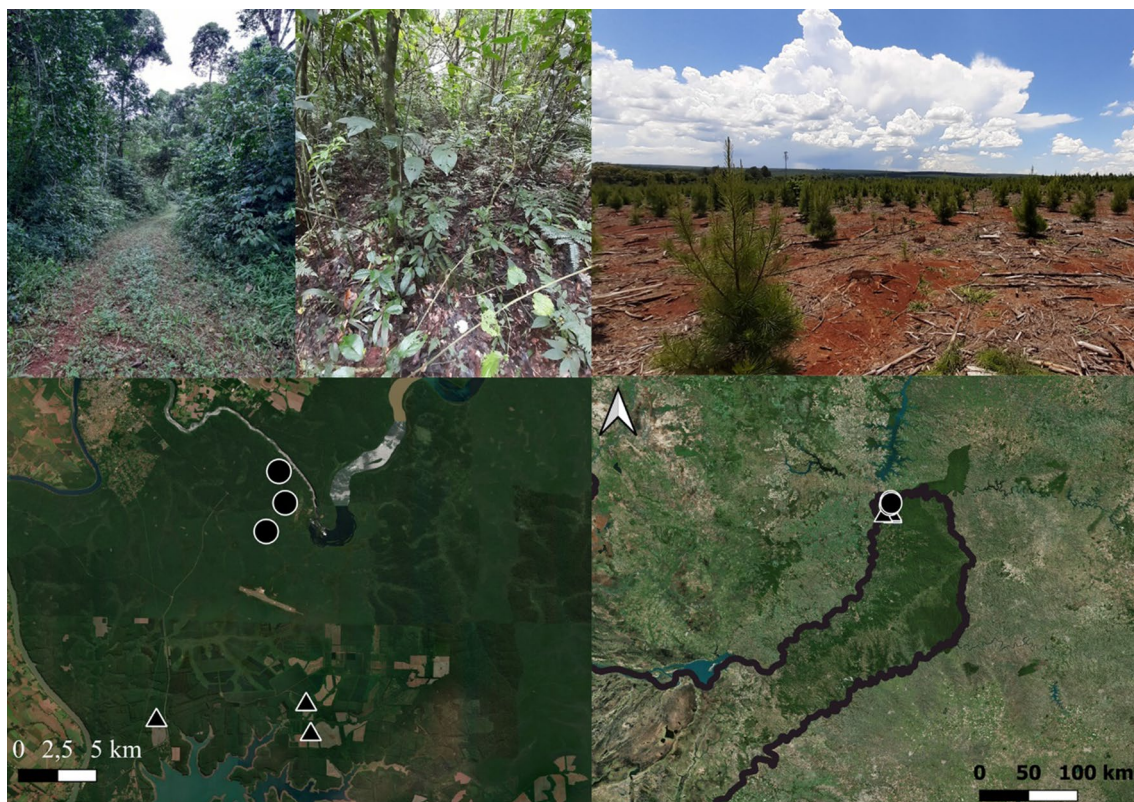


Fig. 1 Spider sampling sites in young pine plantations (triangles) and native forests (circles) in the southern Atlantic Forest of Argentina. Map created using the free and open source QGIS with Bing Aerial (QGIS.org 2023)

continuous forest (Fig. 1). Based on this prior knowledge (presence or absence of species within native forest and young pine plantations), we defined a species as a generalist or specialist according to the presence in both habitats (generalist) or restricted to native forest (specialist). Live individuals were collected during the early spring season: October, November 2021 and August 2022. We collected spiders with the more gentle methods available, to keep spiders as unharmed as possible. We used some of the collecting methods described by Munévar et al. (2018) which were the following: minor and major beating, and nocturnal and diurnal hand collection. Minor and major beating was only performed within the forest because of the absence of the shrubs and low arboreal strata needed for these methods within young pine plantations. We then classified all species into guilds following Dias et al. (2009), where species with similar foraging strategies were grouped (Table 1). We collected adult or subadult individuals from the selected species during fieldwork.

Thermal tolerance measurement

Before measurements, we acclimated individuals in a rearing chamber (Ingelab I-501PF, Buenos Aires, Argentina, Figure S15 b) for five days at 25 ± 0.5 °C and 12 h: 12 h of light–dark cycle (lights on at 8:00 am). We know from previous studies that an acclimation period of 24 h is often sufficient to acclimate insects to novel constant temperatures (Weldon et al. 2011; Phungula et al. 2023), and longer acclimation periods were not feasible due to logistics (use of laboratory time). Our minimum of 5 days of acclimation is within the accepted standard of 5–8 days used in thermal testing for spiders and other species (e.g. Jumbam et al. 2008; Anthony et al. 2021). After acclimation, we weighed each spider to the nearest 0.1 mg using an analytical balance (Explorer E01140, Ohaus, Parsippany, NJ, USA) and placed them individually on a temperature plate (Pelt-plate, Sable Systems International (SSI), Las Vegas, NV, USA) (Figure S15 a2) connected to a temperature controller (Pelt-5; SSI

(Figure S15 a1). On the temperature plate, we placed four spiders, each one individually covered by a Petri dish with its walls coated with fluon® to prevent them from escaping and to ensure that spiders were standing on the plate, minimising any possible bias resulting from a thermal gradient in the air.

Critical thermal minimum and maximum (CTmin and CTmax)

To measure the critical thermal minimum (CTmin), we first placed individuals on top of the temperature plate at 25 °C for five minutes and then set up a descending temperature ramp at a rate of -0.5 °C min^{-1} . This ramping rate was chosen as a careful balance between a slower ramping rate more likely to be experienced in nature and a faster ramping rate that avoids the potentially confounding effect of desiccation associated with long experimental times (Rezende et al. 2011). Although there is evidence that faster heating rates (from 0.1 to 0.5) can lead to higher CTmax in some endothermic and ectothermic insects, and faster cooling rates can lower their CTmin values (Chown et al. 2009), we were primarily interested in assessing the difference between specialist and generalist species without exposing individuals to other stress conditions, as it is dehydration that can result from prolonged exposure to lower rate experimental conditions (Rezende et al. 2011). We define CTmin as the point at which coordinated muscle function was lost, following previously established criteria (Terblanche et al. 2006; de la Vega et al. 2015; de la Vega and Schilman 2018; Belliard et al. 2019). To assess this, we applied mechanical stimulation to the spiders every 30 s using a thin metal filament and recorded the temperature at which they stopped responding.

We performed the same procedure previously described to measure the critical thermal maximum (CTmax) but with an ascending temperature ramp of 0.5 °C min^{-1} . CTmax was determined at the temperature at which the spider stopped moving (knockdown) and did not respond to mechanical stimulation.

Table 1 Selected spider species inhabiting young pine plantations and native forests (generalists) and restricted to native forests (specialists) in the southern Atlantic Forest of Argentina

Guilds	Specialist species	Generalist species
Aerial hunters	<i>Aysha</i> sp. <i>Teudis</i> sp. <i>Peucetia</i> sp.	<i>Cheiracanthium inclusum</i> <i>Oxyopes</i> sp.
Orb weavers	<i>Miagrammopes guttatus</i> <i>Uloborus trilineatus</i> <i>Mangora</i> sp.	<i>Alpaida rubellula</i>
Nocturnal aerial hunters	<i>Ero lata</i> <i>Gelanor zonatus</i>	–
Diurnal space web weavers	<i>Mesabolivar</i> sp. <i>Thwaitesia affinis</i>	–

Species were classified into feeding guilds following Dias et al. (2009)

It is worth mentioning that we used the same spiders to measure both CT_{min} and CT_{max}, ensuring that they received at least three days to recover under controlled conditions of light (12:12 LD) and temperature (25 °C). Importantly, Kaspari et al. (2015) found no evidence of bias in the final estimation of CT_{max} when ramping down for CT_{min} measurements before subsequently ramping upward for CT_{max} measurements in the case of ants. Measuring the same individuals offers the advantage of reducing inter-individual variation and facilitates the calculation of an average and deviation of the thermotolerance range (i.e., CT_{max}–CT_{min}).

Statistical analysis

We first compared the thermal limits between species using a mixed-effects model from the lme4 package with the identity of species (13 species) as a fixed factor (Bates et al. 2015). We include body mass and sex (four levels: male, female, male subadult, female subadult) as covariate and random effect factors, respectively.

To test our prediction that spiders inhabiting both tree plantations and native forests (generalists) will have a wider thermal range (i.e., lower CT_{min} and higher CT_{max} and thermal range) than species restricted to the native forest (specialists), we used mixed-effects models. In this analysis, we included two factors with two levels and their interaction: habitat specialisation (generalists and specialists) and guild (aerial hunters and orb weavers). Thermal tolerance is not independent of body mass, so we included this factor as a covariate and sex as a random effect factor. For CT_{max} and thermal range, we used a mixed linear model because the data showed normality and homoscedasticity. For CT_{min}, we used the lognormal distribution after adding a constant to eliminate negative and zero values. We exclude from this analysis two guilds only present in native forests (nocturnal aerial hunters and diurnal space web weavers). Finally, we fitted the model to a standardised version of the dataset to estimate the standardised parameters of CT_{max} and CT_{min}. We calculate the confidence intervals (5–95%) and the p-values using a Wald t distribution approximation. The fully averaged model coefficients and their significance were generated by the pbkrtest package (Halekoh and Højsgaard 2014). The predicted values were generated by the ggeffects package (Lüdtke 2018).

We repeated these analyses with a phylogenetic approach, for this purpose we constructed a phylogeny with available sequences for the cytochrome c oxidase subunit I gene (COI) in BOLD-System (Ratnasingham and Hebert 2007 <https://www.boldsystems.org/index.php/>) and NCBI-National Center for Biotechnology Information repository (<https://www.ncbi.nlm.nih.gov/>). We selected sequences of species of spiders that belong to the same genera of our species

pool. The tree was constructed by using Geneious software version 7.1.3. The barcoding placements were obtained from a UPGMA tree building method; and Tamura-Nei as the genetic distance method. The tree is available as a Newick file and all information relative to BOLD and NCBI sequences used are detailed in (Table S17).

The Phylogenetic Generalized Linear Mixed Models (PGLMM) approach was used to investigate relationships between microclimatic conditions, habitat type, guilds and critical thermal limits of spiders. The PGLMM::phyr package (Ives et al. 2023) allows to fit a generalized lineal mixed model including the main phylogenetics effects on the covariance of response variable. For our purpose we selected microclimatic conditions as daily maximum, minimum temperatures and thermal amplitude range (amplitude), habitat type (native forest and young pine plantations), spiders guilds (Aerial hunters and Orb weavers), species ID as fixed variables, and body mass as a covariate. Random variables were sex (juvenile females, juvenile males, males and females) and species phylogenetic signal. Response variables were the critical thermal minimum (CT_{min}), maximum (CT_{max}) and thermal tolerance range (thermal range) of spiders. We only show the result from the PGLMM analysis, the GLMM are available in the supplementary material (Figure S12–S14; Table S23–S29).

To compare the microclimatic temperature conditions between native forest and pine plantations, we fitted linear models using Ordinary Least Squares to predict: (a) minimum microhabitat temperature, (b) maximum microhabitat temperature, and (c) thermal range of the microhabitat with habitat type and month as fixed factors; (d) minimum microhabitat temperature, and (e) maximum microhabitat temperature with habitat and hour as fixed factors. We then used the emmeans package (Searle et al. 1980; Lenth 2023) for pairwise post hoc multiple comparisons. Finally, we performed three linear models estimated by ordinary least squares to predict: (a) CT_{min} with minimum microhabitat temperature and habitat type (forest and pine), (b) CT_{max} with maximum microhabitat temperature and habitat type, and (c) CTrange with microhabitat thermal amplitude and habitat type. We performed all statistical analyzes in R software version 4.2.3 (R Core Team 2023).

Results

Microclimatic conditions

During the hottest month of the year (December), the mean maximum temperature in tree plantations was 31 ± 8.8 °C (\pm SD), while in native forests it was 24.95 ± 3.9 °C. During the coldest month of the year (June), the mean

minimum temperature was 15.4 ± 7 °C in tree plantations and 14.6 ± 4.2 °C in native forests.

There was a significant interaction between habitat and month on the mean minimum temperature [LM, $F(19, 75,478) = 1999.11$, $p < 0.001$], the mean maximum temperatures of the microhabitat [LM, $F(19, 75,478) = 2646.07$, $p < 0.001$] and the mean thermal range of the microhabitat [LM, $F(19, 75,478) = 1728.29$, $p < 0.001$]. Young pine plantations had higher mean monthly and daily temperatures than forests (Table S1, Table S2–S5). We observed the highest temperature differences between habitats during December, January, March, and July for minimum temperatures (Fig. 2b; Table S4–S5, Figure S1); from December to April for maximum temperatures (Fig. 2a, Table S2–S3, Figure S2) and thermal range (Fig. 2c, Table S10–S11, Figure S5).

Likewise, there was a significant interaction between habitat and hour (24-h cycle) on mean minimum temperature [LM, $F(47, 75,450) = 893.49$, $p < 0.001$] and mean maximum temperature [LM, $F(47, 75,450) = 1006.10$, $p < 0.001$]. During the 24-h cycle, differences are observed between 8:00 am and 5:00 pm for minimum temperatures (Fig. 3b; Table S6–S7, Figure S3) and between 7:00 am and 8:00 pm for maximum temperatures (Fig. 3a; Table S8–S9, Figure S4). At these times, we observed significantly higher temperatures in pine plantations, especially between sunrise and sunset.

Thermal limits

The species under analysis for Critical Thermal Limits (CTL) do not show any phylogeny nesting according to their degree of specialization, as seen in the phylogenetic tree (Fig. 4).

Without the phylogenetic approach (GLMM), we found a significant effect of species identity on spider thermal tolerance (Figs. 5, S6; Table S12–S16). However, when we performed the same analysis with the phylogenetic approach, we saw no difference between species thermal range. In contrast, we see a strong effect of species identity closely followed by a phylogenetic species effect, (Table S22, Figure S11). Nevertheless, when we compared species by habitat, we see a strong effect of habitat specialization, also there is a strong phylogenetic species effect closely followed by a sex effect (Table S21, Figure S10).

Under the phylogenetic approach, we see a significant effect of spider habitat specialization and the interaction between variables (habitat specialization and guild) on CTmax, CTmin, and thermal tolerance range (Fig. 6; Table 2, S18–S20). We found no effect of guild type on CTmax (Table 2) and no effect of microclimatic conditions on thermal limits (CTmax, CTmin and thermal range). We obtained the same results when evaluating the effect of

habitat type and microclimatic temperature conditions on thermal limits with linear models (Table 3; Fig. 7).

In the case of CTmax, generalist species of both guilds showed higher tolerance; however, due to the significant effect of the interaction, this effect was more pronounced in orb-weavers than in aerial hunters (Fig. 6a; Figure S8; Table 2, S19). CTmin showed a similar pattern, being lower in generalist species than in specialists, and the effect was more pronounced in orb weavers than in aerial hunters (Fig. 6b; Figure S7; Table 2, S18). Finally, generalist species showed a higher thermal tolerance range (CTmax–CTmin) than specialist species, with a more pronounced effect in orb weavers than in aerial hunters (Fig. 6c; Figure S9; Table 2, S20).

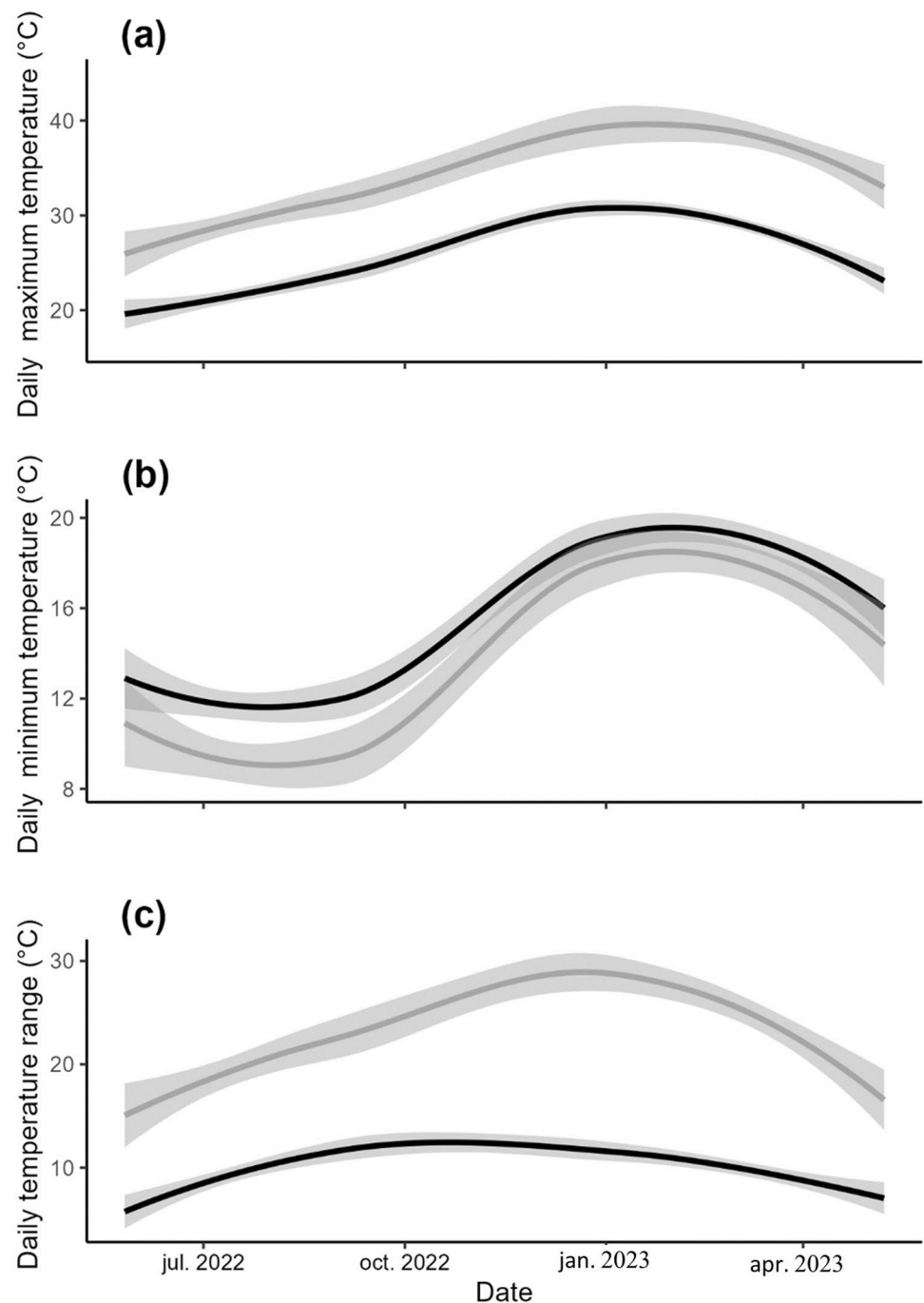
Discussion

Our results support the hypothesis that habitat specialists are more vulnerable to human disturbance of natural ecosystems than native generalist species (Vázquez and Simberloff 2002; Wilson et al. 2008); and that thermal tolerance is an important physiological response trait to explain the ability (or inability) of native organisms to colonize and persist in disturbed habitats (Angilletta et al. 2002; Angilletta 2009). However, other dimensions of the ecological niche (trophic specialization, and nesting requirements, among others) may also have an important role in the colonisation of disturbed habitats by native species. In line with our predictions, spiders restricted to native forests showed lower thermal tolerance than species from pine plantations. Furthermore, our results provide a mechanistic explanation for the drastic reduction in species richness and changes in species composition after forest replacement by tree plantations in the southern Atlantic Forest (Munévar et al. 2018; Cifuentes-Croquevielle et al. 2020); and probably in other land uses and ecosystems (Aratrakorn et al. 2006; Harvey and González Villalobos 2007; Lebrija-Trejos et al. 2008; Durak et al. 2015).

In general, previous studies found higher variability of lower thermal limits (CTmin) than upper thermal limits (CTmax) for ectotherms, plants and endotherms (Araújo et al. 2013). However, we found high variability in upper and lower thermal limits. Species with stable geographic ranges or low range expansion, such as the species we studied, are expected to be locally adapted such that their thermal limits stabilize at values appropriate for their immediate environment (Lancaster 2016); this may explain the high variability as each species occupies a different microhabitat (e.g., low stratum vegetation, more open vegetation, etc.).

Our results in spiders show that the upper and lower thermal limits and the thermal tolerance range do not have a significant correlation with thermal microclimate conditions

Fig. 2 Daily thermal microclimatic conditions within native forests (in black) and pine plantations (in grey) in the southern Atlantic Forest of Argentina with 95% CI. Mean daily maximum temperature (a), mean daily minimum temperatures (b), and mean daily temperature range (c)

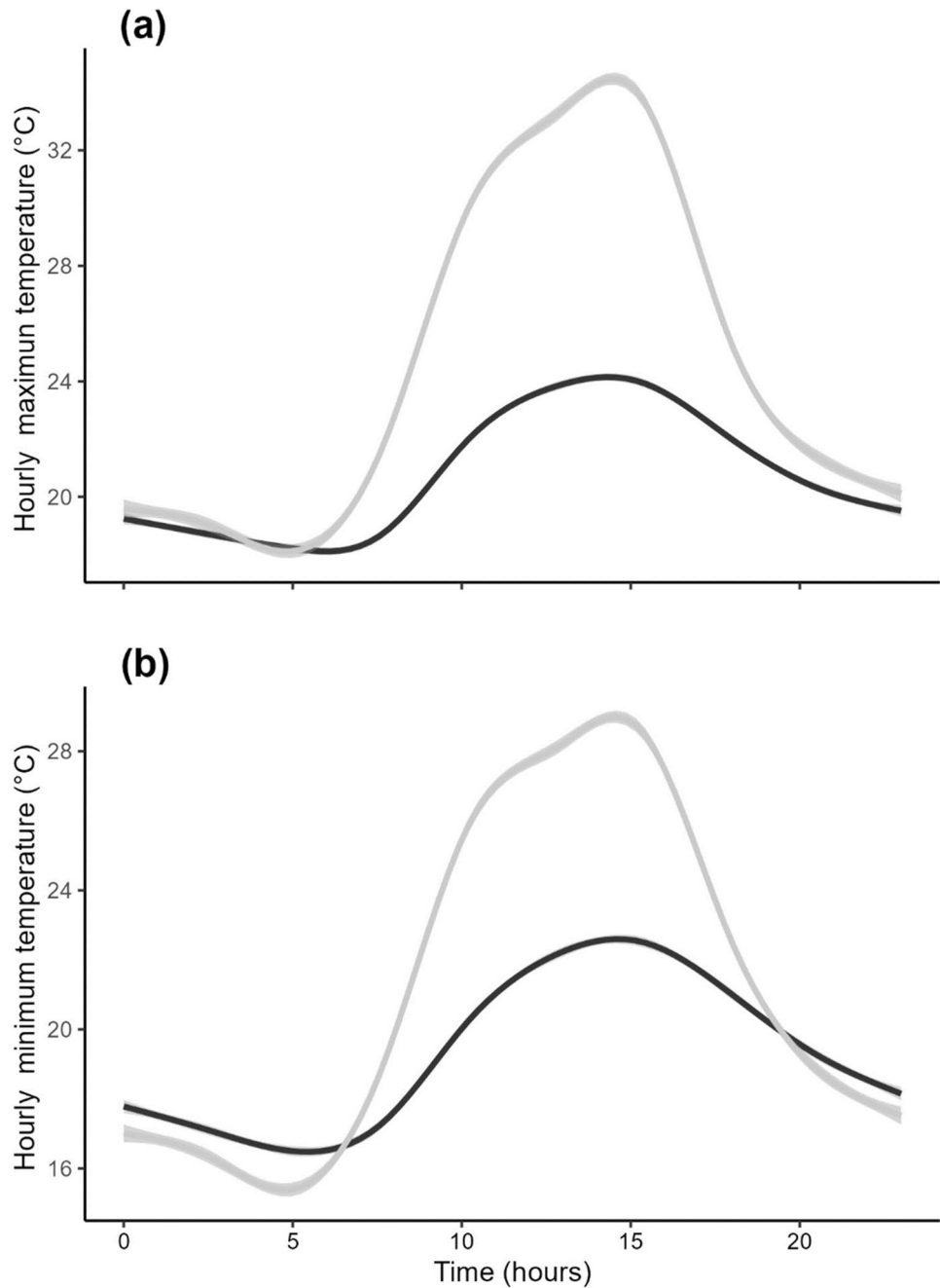


in forests and young pine plantations. Similar trends are observed in the literature. In a study of 132 ant species from North America and other ectotherms worldwide, the upper thermal limits and the thermal tolerance range did not covary with environmental temperature, whereas the lower thermal limits did. These authors suggest that natural selection strongly modulates the physiological response to lower than upper temperatures and that upper thermal limits are better explained by habitat, phylogenetic signal and species expansion range than by environmental temperature (Araújo

et al. 2013; Bujan et al. 2020). In another global meta-analysis of ants, the upper and lower thermal limits covaried with environmental temperatures. However, the strongest effect was attributed to the phylogenetic history for upper thermal limits rather than geographic variation in temperature (Diamond and Chick 2018).

Although this is the first study on spider thermal tolerance in tree plantations, our results are consistent with previous studies on other ectotherms, showing that forest specialist species have lower thermal tolerance than generalist species

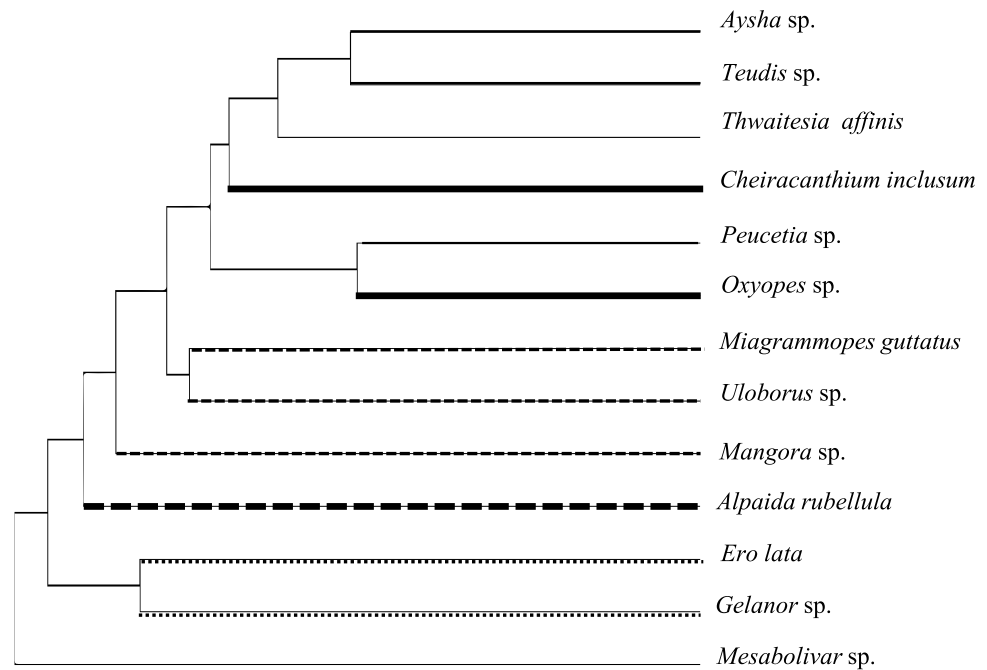
Fig. 3 Variation in thermal microclimatic conditions during the 24-h cycle within native forest (in black) and pine plantations (in grey) in the southern Atlantic Forest of Argentina with 95% CI. Average hourly maximum temperature (a) and mean hourly minimum temperatures (b)



(Nowakowski et al. 2017; Barahona-Segovia et al. 2019, 2022; Woon et al. 2022; Bota-Sierra et al. 2022). Furthermore, other ectotherms exhibit differences in thermal tolerance across microclimates. For example, ants nesting in the canopy had an average CT_{max} of 3.5 to 5° C higher and were active over a greater range of temperatures than populations that nested in the shade of the understory (Kaspari et al. 2015, 2016). In different habitats, nocturnal ants had a lower CT_{max} than diurnal species (García-Robledo et al. 2018). Furthermore, the nocturnal species of dung beetles showed significantly lower CT_{min} than the crepuscular and

diurnal species (Gotcha et al. 2021; Giménez Gómez et al. 2020). Although in dragonflies and damselflies (order Odonata), lower thermal tolerance (CT_{min}) is not associated with temperatures prevalent at different elevations and habitats used, upper thermal limits (CT_{max}) are (Bota-Sierra et al. 2022). Furthermore, forest Odonata species displayed lower thermal tolerances than open-area species (Bota-Sierra et al. 2022). These results suggest that local thermal conditions experienced in natural or simplified habitats influence the thermal response of ectotherms and, consequently, their

Fig. 4 Phylogeny of the spiders used in this study; the tree was developed based on available sequences for the cytochrome c oxidase subunit I gene (COI) in BOLD-System (Ratnasingham and Hebert 2007 <https://www.boldsystems.org/index.php/>) and NCBI-National Center for Biotechnology Information repository (<https://www.ncbi.nlm.nih.gov/>). Thicker lines (pine plantations species), thinner lines (native forest species). Dashed lines: denote the orb weaver's guild, continuous thick lines: aerial hunters; thinner continuous lines: diurnal space web weavers and, dotted lines: nocturnal aerial runners



tolerance (Hoffmann and Sgrò 2018; Abram et al. 2017), but are not the only drivers.

Young pine plantations show temperature variations with extremely high temperatures in summer, low temperatures in winter, and enormous daily temperature variability. On the contrary, native forests have more stable conditions. These thermal differences suggest that species living in young tree plantations have mechanisms such as better thermal tolerance to survive more fluctuating thermal conditions. In a similar previous study with dung beetles in the southern Atlantic Forest, only diurnal native species with active thermoregulatory mechanisms or nocturnal species were able to colonize and persist in open habitats (Giménez Gómez et al. 2020). In the case of spiders, differences in colouration, cuticle wax, or other physiological adaptations could explain the different tolerance of specialist and generalist species (Riechert 1976; Cloudsley-Thompson 1983; Rao and Mendoza-Cuenca 2016; Malmos et al. 2021).

Although the response was consistent across habitat specialisation (higher tolerance of generalists over specialists), the response was more pronounced in orb weavers than aerial hunters. These differences between guilds may reflect different mechanisms for tolerating high and low temperatures among spiders with different foraging strategies (Krakauer 1972). Aerial hunters are active foliage-dwelling spiders that hunt in vegetation (Dias et al. 2009), whereas orb weavers have a more passive hunting method based on the web they use (Dias et al. 2009). Based on these different behaviours, we expected that species of the more active guild (aerial hunters) would have a lower thermal tolerance range than

the stationary one (orb weavers), as there is a trade-off between physiological response mechanisms and behavioural response (in this case, the ability to move out of an unfavourable thermal location quickly) (Bogert 1949). However, we observed this pattern only within tree plantations. We believe that within the forest, the location and orientation of orb weavers' webs play a key role, as orb weavers are probably selecting sites with optimal thermal conditions and, in this way, relaxing physiological responses (Riechert 1976; Cloudsley-Thompson 1983). In contrast, aerial hunters, due to their evolved tracheal system, which gives them speed and flexibility of movement, are actively shifting between optimal and suboptimal thermal sites as they forage (Dias et al. 2009; Brescovit 1996). Therefore, equally prioritising both behavioural and physiological thermoregulation.

In addition, web-building spiders may be more susceptible to heat-related mortality than more mobile organisms. Adult females of many spider families are sedentary, building webs in microhabitats where they spend their entire lives. In extreme heat, they may be limited in their ability to move vertically or horizontally to find cooler microhabitats. Males, on the other hand, are often nomadic, have a wider spatial distribution and may be better able to escape heat. However, life history traits in spiders, such as the relative body size and spatial ecology of males and females, also vary between taxonomic groups based on their phylogeny. This may make different species or families more or less susceptible to heat waves and exposure to very high temperatures. Selection for extreme temperatures may drive adaptive responses in female physiology, morphology or web site selection in species that build small or exposed webs. Male

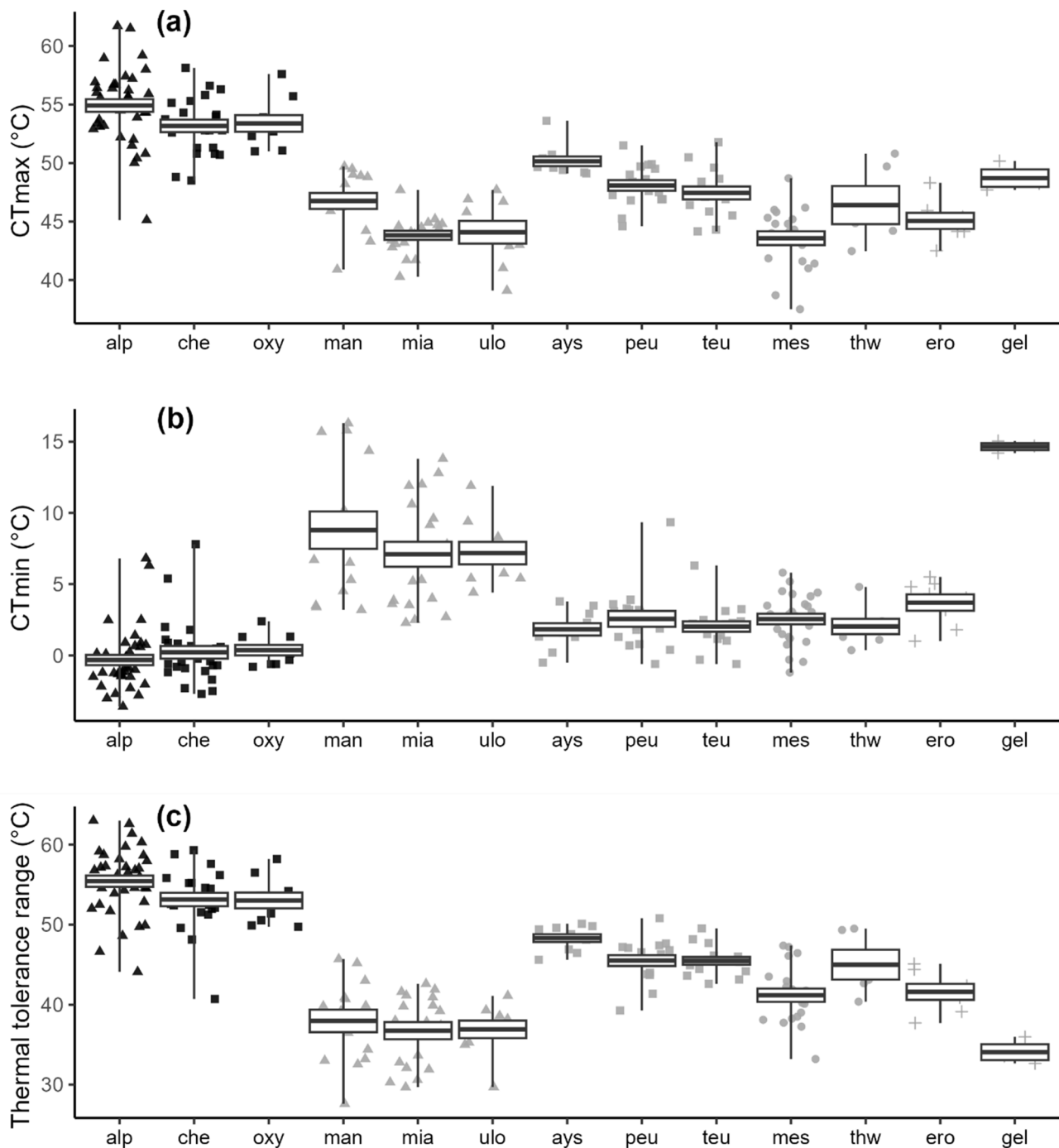


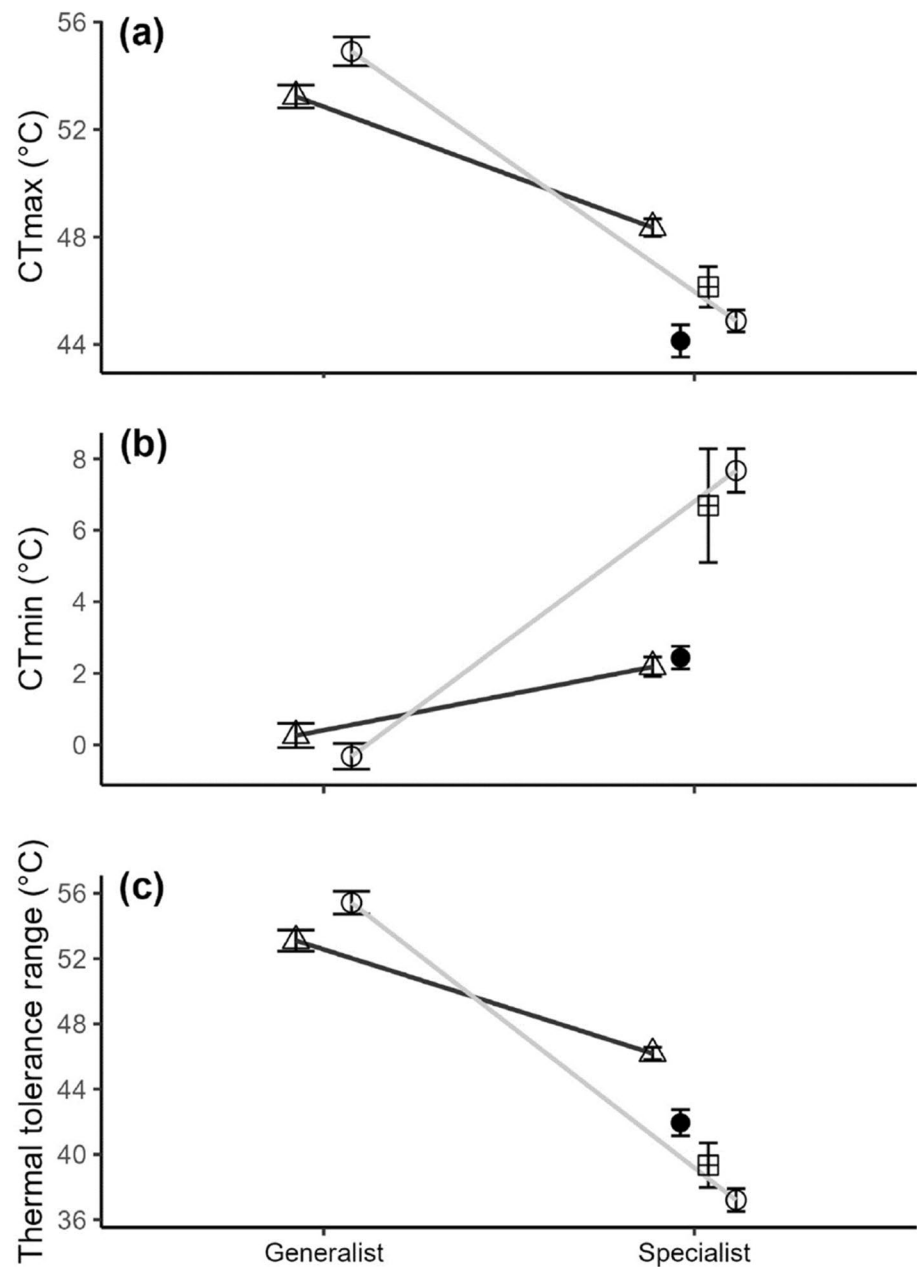
Fig. 5 Critical thermal maximum (a), minimum (b), and thermal tolerance range (c) with means \pm SE, max and min values given by boxplot and whiskers of 13 species from 4 guilds (triangle: orb weavers, square: aerial hunters, plus: nocturnal aerial hunters and circle: Diurnal space web weavers). Species inhabiting both tree plantations and native forests (generalists: black symbols), and restricted to the

native forest (specialists: grey symbols) in the southern Atlantic Forest of Argentina. Each point represents a unique specimen. alp: *Alpaida rubellula*; che: *Cheiracanthium inclusum*; oxy: *Oxyopes* sp.; ays: *Aysa* sp.; man: *Mangora* sp.; mia: *Miagrammopes guttatus*; ulo: *Uloborus* sp.; peu: *Peucetia* sp.; teu: *Teudis* sp.; mes: *Mesabolivar* sp.; thw: *Thwaitesia affinis*; ero: *Ero lata*; gel: *Gelanor* sp.

spiders may be better able than females to avoid heat stress by seeking shelter under objects such as bark or rocks with cooler microclimates. Conversely, males may not be able to build webs, or adult males may have to leave them to find

females for reproduction. This not only exposes them to risks from visually foraging predators that use movement as a cue, but also means that males can occupy much wider thermal niches than females (Harvey and Dong 2023).

Fig. 6 Thermal tolerance of spiders that are restricted to native forests (specialists) and species that inhabit both tree plantations and native forests (generalists) in the southern Atlantic Forest of Argentina. Triangles: Aerial hunters; white circle: Orb weavers; filled circle: Diurnal space web weavers; square plus: Nocturnal aerial runners



Our results may help to improve the design of tree plantations in the southern Atlantic Forest to increase the suitability of this land use for spiders and other arthropods. As thermal tolerance in spiders is associated with microhabitat selection (DeVito et al. 2004), we suggest that young plantations should retain as much complexity as possible to maintain thermally favourable microhabitats for other spiders. Munévar et al. (2018) found a rapid increase in the suitability of pine plantations after 5–6 years, coinciding with a decrease in understory temperature after canopy closure. Furthermore, there is a difference in spider ecology depending on the sex in the case of species that present sexual dimorphism.

Thermal effects on organisms extend beyond critical survival thresholds. Recently, attention has focused on thermal fertility limits (TFL) at which reproduction may be impaired or terminated. The upper TFL for insects is often lower than CTmax, meaning that male or female organisms do not necessarily die, but their eggs and/or sperm are destroyed, rendering them sterile (Parratt et al. 2021; Walsh et al. 2021; Harvey et al. 2023). Spiders have a complex reproductive cycle in which males transfer fully encapsulated sperm from the gonopore to a sperm web into which they dip their palps and load them with sperm, which is then injected into the female epigynum, after which it is de-encapsulated (Dharmarathne and Herberstein 2022). It remains to be

Table 2 Phylogenetic Generalized Linear Mixed Models model testing the effect of habitat specialisation (generalists-specialists) and guild type (aerial hunters and orb weavers) on the thermal tolerance of spiders in the southern Atlantic Forest of Argentina

Fixed effects	Estimates	Std. Error	Z	p
<i>CT_{max} °C</i>				
Habitat specialisation [generalist] × guild [ow]	56.94	3.32	17.15	< 2.2e−16***
Max. temp. microhabitat	− 0.036	0.07	− 0.52	0.599
Habitat specialisation [specialist] guild [ah]	− 10.63	1.55	− 6.84	8.017e−12***
Body mass	− 1.532	1.51	− 1.014	0.31
Habitat specialisation [specialist] × guild [ah]	− 0.016	0.03	− 0.43	0.66
Habitat specialisation [specialist] × guild [ah]	5.315	1.78	2.98	0.00287 **
<i>Log (CT_{min} + 5 °C)</i>				
Habitat specialisation [generalist] × guild [ow]	1.5223	0.0959	15.87	< 2.2e−16***
Min temp microhabitat	0.00052	0.0069	0.0754	0.93992
Habitat specialisation [specialist] guild [ah]	0.9818	0.0846	11.59	< 2.2e−16***
Body mass	0.1875	0.0811	2.31	0.02086*
Habitat specialisation [specialist] × guild [ah]	− 0.0067	0.0047	− 1.42	0.155
Habitat specialisation [specialist] × guild [ah]	− 0.5805	0.1239	− 4.685	2.792e−06***
<i>Thermal tolerance range °C</i>				
Habitat specialisation [generalist] × guild [ow]	58.75	3.71	15.84	< 2e−16 ***
Microhabitat thermal amplitude	− 0.07	0.08	− 0.79	0.424
Habitat specialisation [specialist]	− 19.27	1.26	− 15.3	< 2e−16***
Guild [ah]	− 2.235	0.95	− 2.33	0.019*
Body mass	− 0.028	0.05	− 0.53	0.59
Habitat specialisation [specialist] × guild [ah]	11.62	1.39	8.34	< 2e−16***

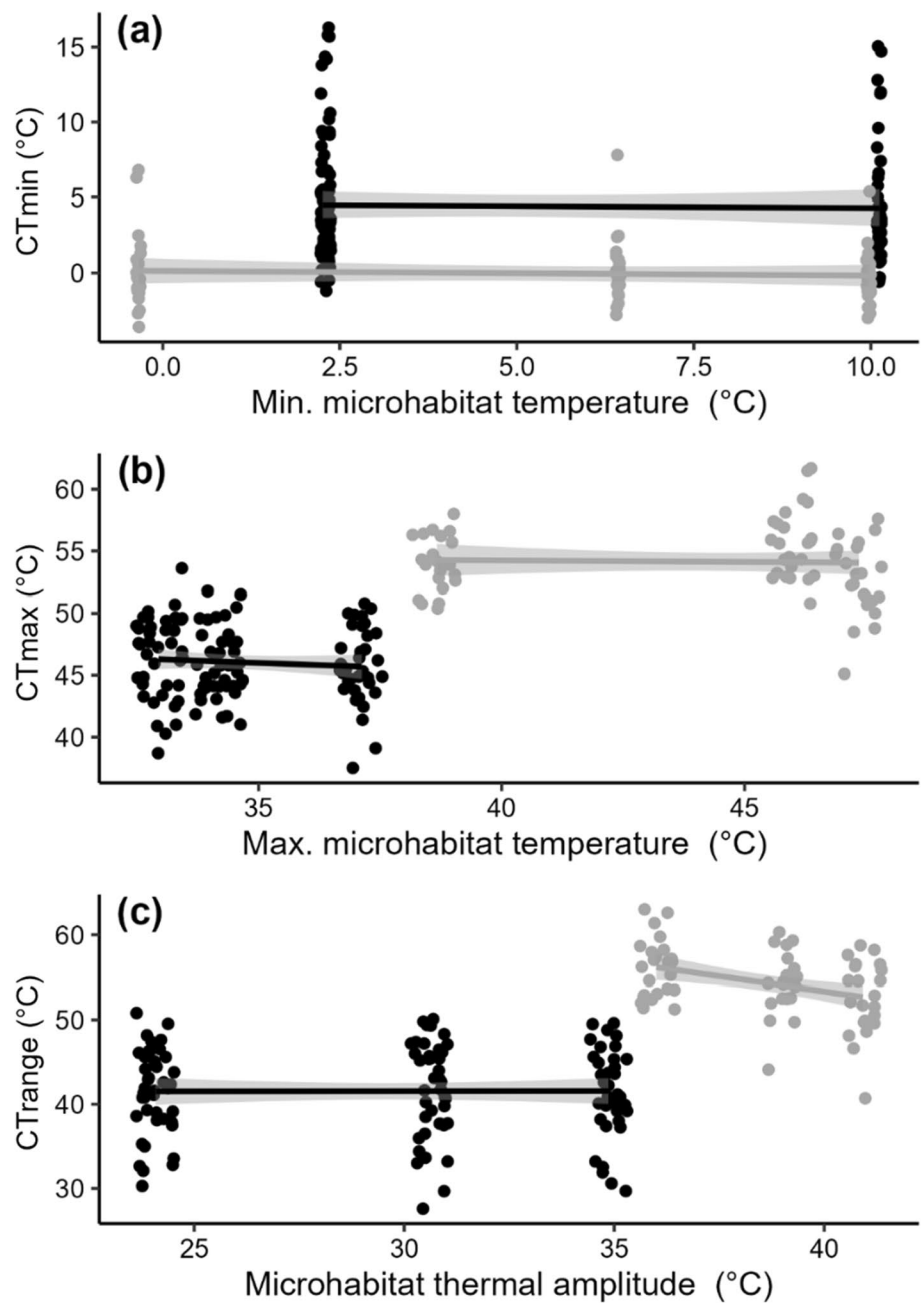
Table 3 Linear model testing the effect of microhabitat temperature (maximum, minimum, and thermal amplitude) and habitat specialization (generalists-specialists) on the thermal tolerance of spiders in the southern Atlantic Forest of Argentina

Fixed effects	Estimates	CI	Statistic	p
<i>CT_{min} °C</i>				
Habitat[Forest]	4.59	3.74 to 5.44	10.64	< 0.001
Min. microhabitat temperature	− 0.03	− 0.15 to 0.09	− 0.45	0.65
Habitat [pine]	− 4.47	− 5.47 to − 3.48	− 8.83	< 0.001
Observations	199			
R2/R2 adjusted	0.288/0.281			
<i>CT_{max} °C</i>				
Habitat[Forest]	48	42.18 to 53.81	16.29	< 0.001
Max. microhabitat temperature	− 0.06	− 0.22 to 0.11	− 0.66	0.507
Habitat [pine]	8.62	6.79 to 10.45	9.31	< 0.001
Observations	184			
R2/R2 adjusted	0.627/0.623			
<i>Thermal tolerance range °C</i>				
Amplitude × Habitat [forest]	41.43	35.41 to 47.45	13.57	< 0.001
Amplitude	0	− 0.20 to 0.20	0.04	0.97
Habitat [pinar]	40.14	17.31 to 62.98	3.47	0.001
Amplitude × Habitat [pine]	− 0.71	− 1.31 to − 0.10	− 2.32	0.022
Observations	184			
R2/R2 adjusted	0.625/0.619			

studied whether sperm could be more vulnerable to thermal extremes along this complex fertilization process in spiders and other arthropods. Future studies would aim to include more species from different strata, such as ground-dwelling species (Munévar et al. 2018). Furthermore,

specific physiological or morphological traits (such as the cuticle) associated with this differential tolerance should be

Fig. 7 Relation between thermal limits, environmental temperature and the degree of habitat specialization in the southern Atlantic Forest of Argentina. Lines represent the fits of Ordinary Least Squares regression for specialist (black symbols) and generalist (dark grey symbols) species separately with 95% confidence bands (grey shading)



investigated, as well as the effect on thermal fertility limits (TFL) in spiders and other arthropods.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00442-024-05529-8>.

Acknowledgements We would like to thank the National Scientific and Technical Research Council (CONICET/Argentina). The National Park Administration and the Misiones Ecology Ministry gave the necessary permissions for fieldwork. YMGPE has a doctoral fellowship from CONICET. We thank Jeffrey A. Harvey and an anonymous reviewer whose constructive criticisms improved the paper.

Author contributions statement YMGPE, PES, and GAZ conceived the ideas and designed the methodology. YMGPE and AM collected the data and performed the analyses. All authors critically contributed to the drafts and gave their final approval for publication.

Funding This work was supported in part by the National Agency for the Promotion of Science and Technology of Argentina (ANPCyT) [PICT 2018-02810 to PES], the University of Buenos Aires (UBA) [UBACyT-20020190200278BA to PES], CONICET (PIP-11220200102397CO to PES and PUE2016 to M. Di Bitetti).

Availability of data and materials The data was deposited in figshare under the reference number <https://figshare.com/s/9418a4b359e9122a5594>.

Code availability Not applicable.

Declarations

Conflict of interest None of the authors declared a conflict of interest.

Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed. Research authorisation DRNEA-516-Zurita, Gustavo: IF-2021-87003069-APN-DRNEA#APNAC, IF-2022-118456099-APN-DRNEAAPNAC.

Consent to participate Not applicable.

Consent for publication (include appropriate statements) Not applicable.

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