

RESEARCH ARTICLE

Climate change and invasive species: a physiological performance comparison of invasive and endemic bees in Fiji

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ABSTRACT

Anthropogenic climate change and invasive species are two of the greatest threats to biodiversity, affecting the survival, fitness and distribution of many species around the globe. Invasive species are often expected to have broad thermal tolerance, be highly plastic, or have high adaptive potential when faced with novel environments. Tropical island ectotherms are expected to be vulnerable to climate change as they often have narrow thermal tolerance and limited plasticity. In Fiji, only one species of endemic bee, *Homalictus fijiensis*, is commonly found in the lowland regions, but two invasive bee species, *Braunsapis puangensis* and *Ceratina dentipes*, have recently been introduced into Fiji. These introduced species pollinate invasive plants and might compete with *H. fijiensis* and other native pollinators for resources. To test whether certain performance traits promote invasiveness of some species, and to determine which species are the most vulnerable to climate change, we compared the thermal tolerance, desiccation resistance, metabolic rate and seasonal performance adjustments of endemic and invasive bees in Fiji. The two invasive species tended to be more resistant to thermal and desiccation stress than *H. fijiensis*, while *H. fijiensis* had greater capacity to adjust their CT_{max} with season, and *H. fijiensis* females tended to have higher metabolic rates than *B. puangensis* females. These findings provide mixed support for current hypotheses for the functional basis of the success of invasive species; however, we expect the invasive bees in Fiji to be more resilient to climate change because of their increased thermal tolerance and desiccation resistance.

KEY WORDS: Desiccation resistance, Global warming, Native bees, Plasticity, Pollinators, Thermal tolerance

INTRODUCTION

The effects of climate change and globalisation are causing an increase in the rate and extent of species invasions across the world, which will have profound consequences for native ecological

communities (Chown et al., 2012, 2007; Logan et al., 2019). Invasive species can impact native communities via changes to competition and predation, spread of disease, and disruptions to plant–pollinator networks (Charles and Dukes, 2008; Crowl et al., 2008; Gallardo et al., 2016; Logan et al., 2019; Molnar et al., 2008). Life history traits such as high fecundity, fast growth rate and greater dispersal capabilities are often implicated in the success of highly invasive species (Sakai et al., 2001; Van Kleunen et al., 2010). But, the physiological traits which govern the climates that organisms can persist in are likely to play key roles in determining which species become invasive (Kelley, 2014).

The physiological factors that are associated with invasiveness allow species to survive in habitats that are climatically different to where they evolved (Broennimann et al., 2007; Tepolt and Somero, 2014). These include: broad thermal tolerance, permitting organisms to persist across a wide range of environmental temperatures and survive rapid thermal change (Zerebecki and Sorte, 2011); high levels of plasticity (acclimatisation), allowing invasive species to adjust their phenotype with changes in climate (Braby and Somero, 2006; Chown et al., 2007; Kelley, 2014; Tepolt and Somero, 2014); and high adaptive potential when faced with new environments (Davidson et al., 2011; Logan et al., 2019). While it is expected that greater thermal tolerance and plasticity are the cornerstones of an invasive phenotype, the extent to which this is true is not well established empirically (Kelley, 2014).


Tropical ectotherms with narrow latitudinal ranges are likely to be among the most susceptible species to climate change as they often live near their upper thermal limits (Kellermann et al., 2012b; Somero, 2010), have narrow thermal tolerance and can have limited acclimation capacities (Deutsch et al., 2008; Tewksbury et al., 2008). The latitudinal range that a species inhabits is often hypothesised to be correlated with either their thermal performance breadth (the range of temperatures an organism can adequately function within) or their capacity to acclimatise with thermal change (Braby and Somero, 2006; Tepolt and Somero, 2014; Zerebecki and Sorte, 2011). Yet, there are few empirical studies that compare the physiological and environmental tolerance of taxonomically similar species that differ in the extent to which they are able to extend their distributions (i.e. invasive or restricted) (Zerebecki and Sorte, 2011). Traits such as critical thermal maximum and minimum, desiccation resistance and metabolic rate are thought to be important for predicting species vulnerability to climate change, and are often used to compare the susceptibility of similar species to climate change (Kellermann and van Heerwaarden, 2019; Seebacher et al., 2015).

Throughout the Fijian archipelago, there is only one endemic bee species that commonly occurs in the lowland region (below 300 m above sea level), the halictid *Homalictus fijiensis* (Perkins and Cheesman) (Fig. 1A) (Dorey et al., 2020; Dorey et al., 2019). With 78% of the remaining natural forests in Fiji occupying lowland regions

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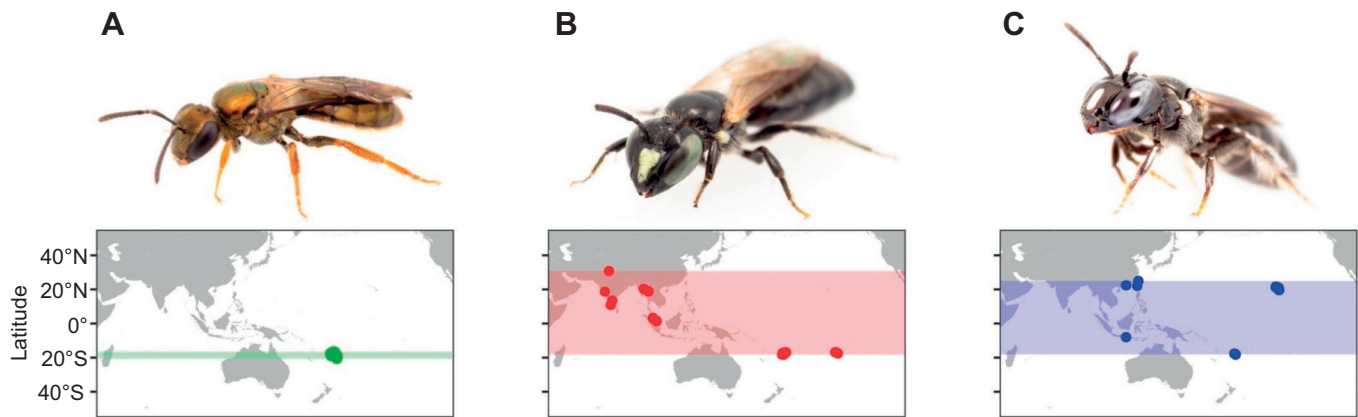


Fig. 1. Photographs of female bees and their distribution. Circles indicate geographic distribution range and shading indicates total latitudinal range for (A) endemic *Homalictus fijiensis*, (B) invasive *Braunsapis puangensis* and (C) invasive *Ceratina dentipes*. Distributional range was calculated from the Global Biodiversity Information Facility (www.gbif.org) and Fijian locality records collected in this study and from data collected by Groom et al. (2015) and da Silva et al. (2016). Bees were photographed by J.B.D.

(Fiji's State of Environment Report 2013, <https://macbio-pacific.info/wp-content/uploads/2017/08/State-of-Environment-Report-2013.pdf>), it is essential to monitor the functioning of these ecosystems to limit biodiversity loss. *Homalictus fijiensis* is a ground-nesting, multivoltine, short-tongued polylectic bee (pollinates multiple plant species) (Crichton et al., 2019), and is probably an important pollinator within natural and agricultural Fijian systems. Their latitudinal range is very narrow ($\sim 4^\circ$), as they are restricted to the Fijian archipelago, and thus theoretically are predicted to be more vulnerable to climate change than species with broad latitudinal ranges.

Within the last 2–3 decades, two invasive stem-nesting Apidae bee species were unintentionally introduced into Fiji, *Braunsapis puangensis* (Cockerell) and *Ceratina dentipes* Friese (da Silva et al., 2016; Groom et al., 2015) (Fig. 1B,C). *Braunsapis puangensis* is distributed in India and south eastern Asia (da Silva et al., 2016; Groom et al., 2015), and is believed to have entered Fiji via shipping containers carrying the ornamental plants that they nest within from India (da Silva et al., 2016). *Ceratina dentipes* is likely to have originated from the Indonesian archipelago and is spreading throughout the Pacific, also probably via anthropogenic dispersal (Groom et al., 2014; Rehan et al., 2010; Shell and Rehan, 2019). These long-tongued species are now commonly found throughout Fijian lowland habitats and have the ability to pollinate both endemic Fijian plants and invasive weed species (da Silva et al., 2016). Their spread throughout Fiji has been extensive and is likely to affect pollination networks and terrestrial ecosystem function throughout the South West Pacific (da Silva et al., 2016; Silva et al., 2017). The latitudinal ranges of both *B. puangensis* (49°) and *C. dentipes* (43°) exceed well beyond that of *H. fijiensis* ($\sim 4^\circ$), as they have invaded many other surrounding countries (Fig. 1).

The combined effects of climate change and invasive alien species are likely to interact and negatively affect native organisms (Chown et al., 2012, 2007; Logan et al., 2019). This is because the predicted characteristics that are thought to make species invasive (higher plasticity/broad thermal tolerance) are likely to make them more resilient to climate change than endemic species with potentially narrow thermal tolerance or limited capacity to acclimatise. Nevertheless, the extent to which invasive alien species possess these physiological characteristics remains poorly tested, meaning we do not know the extent to which invasive alien species will affect native ecosystems with accelerated climate change. Here, we compared the thermal tolerance [critical thermal

maximum (CT_{max}) and chill coma recovery], desiccation resistance and metabolic rate of the invasive bees *B. puangensis* and *C. dentipes* with the geographically restricted endemic bee, *H. fijiensis*. We assessed CT_{max} and desiccation resistance across the wet season (April) and the dry season (September–October) in 2019. Because we cannot rear these bees under controlled conditions, we used seasonal comparisons to determine whether these species have the capacity to shift performance traits across seasons. We used these seasonal shifts as a proxy for plasticity while also acknowledging that these measures are not plasticity in the true sense. Nevertheless, all three bee species were collected across the same sample sites across both the wet and dry seasons, and were exposed to the same experimental techniques. By examining the physiological differences between invasive and an endemic bee species in Fiji, we aim to predict which species are likely to be vulnerable to climate change.

We propose three main hypotheses: (1) the invasive alien species will have broader thermal tolerance than the endemic *H. fijiensis* because of their broader latitudinal range and ability to successfully colonize new environments; (2) the invasive alien species will have greater capacity to seasonally adjust their physiological traits (acclimatise) in comparison to *H. fijiensis*; and (3) energy expenditure (measured as routine metabolic rate) will be greater in the invasive bee species than in the endemic species. Invasive alien species often have higher rates of growth and fecundity than endemic species (Sakai et al., 2001; Van Kleunen et al., 2010), and we expect that, in alignment with the ‘increased intake’ hypothesis (Boratyński and Koteja, 2010; Burton et al., 2011; McMahon, 2002), this potentially greater growth and reproductive capacity will be reflected by higher rates of energetic expenditure in the invasive bee species.

MATERIALS AND METHODS

Animal collection

All bees were collected on Viti Levu (Fiji's largest island) at altitudes below 300 m above sea level between 15 and 20 April 2019 (warm wet season) and from 4 September to 31 October 2019 (cool dry season) (GPS coordinates and collection dates included in the deposited data at <https://doi.org/10.26180/13347173>). In April, the mean maximum air temperature is 30.6°C , with $\sim 6^\circ\text{C}$ daily thermal variation, and there is an average accumulation of 294 mm of rain throughout the month. During September and October, the mean maximum air temperature is 27.2°C , with $\sim 6^\circ\text{C}$ of daily

thermal variation, and there is an average of 137 mm of rain throughout the month (<https://www.timeanddate.com/weather/fiji/suva>; Ongoma et al., 2020). Bees were collected by sweep-netting managed gardens, road verges and native vegetation, or by collecting whole stem nests in small trees and bushes. *Apis mellifera* (European honeybees) are also present in Fiji but were not included in this study. As bees were collected opportunistically, sample sizes varied for each species and performance trait and are reported in each performance trait figure (sex-specific sample sizes are stated in Figs S1–S3). Bees that were collected by sweep-netting were placed into vials immediately upon capture and stored in a cool, dark container for transport back to the laboratory. Bees collected within stem nests (*B. puangensis* and *C. dentipes*) were trapped in the nests with a piece of masking tape covering the nest entrance and were also stored in a cool dark container until processing. Bees collected in the dry season were provided with a small piece of paper towel dipped in 20% sugar water solution during preparation for testing. While we did not do this for the wet season, the addition of sugar water is unlikely to influence our estimates of thermal resistance (Oyen and Dillon, 2018). CT_{max} and desiccation resistance were tested across both the wet and dry season. Chill coma recovery and metabolic rate were only tested in the dry season. All trait measurements were conducted within 3 h of collection. Species and sex were recorded for each specimen through visual assessment (Michener, 2000), where males have 12 antennal segments and females have 13 antennal segments and scopa on their hindlegs or abdomen. *Homalictus fijiensis* are metallic green without face markings; *B. puangensis* are matte black, with females displaying a cream-coloured T-shaped face marking, while males have a filled, cream-coloured figure-of-eight face marking; *C. dentipes* are also matte black, but are slightly smaller than *B. puangensis*, with females having a white line face marking (see Fig. 1 for examples).

CT_{max}

Individual bees were placed into 5 ml airtight glass vials with unique identification numbers. Specimens were placed onto a rack where species and sex were randomised (80 specimens per rack). The rack was placed into a 25°C glass water bath for bee observation (assay started at 25°C as it is an intermediate temperature that bees commonly experience in Fiji). CT_{max} was scored by gradually heating the water bath by 0.1°C per minute (Chown et al., 2009; Kellermann and van Heerwaarden, 2019), where individuals were watched continuously and the CT_{max} of each individual was recorded as the temperature at which they became completely unresponsive and lost the ability to move. CT_{max} outliers below 37°C were likely to be the result of stressed specimens or those that were injured during collection and were removed from the analysis. Removal of these outliers did not impact the analysis (i.e. models with and without outliers reached the same conclusions).

Chill coma recovery

Individual bees were placed into 5 ml airtight plastic Eppendorf® tubes with unique identification numbers and were randomised in the same fashion as for the CT_{max} assay. The rack was placed in an insulated ice bath and held at –1°C for 2 h. Bees were then removed and placed into a 25°C water bath. Recovery time was scored as the length of time it took for each individual to right itself.

Desiccation resistance

Individual bees were placed into a 5 ml vial with gauze over the top to maintain airflow, and then into a rectangular rack (up to 300

specimens per rack) where species and sex were randomised. The rack was placed within a desiccation chamber (glass tank containing silica gel; relative humidity <5%; see Kellermann et al. 2012a) and maintained at 25±2°C (indoor air conditioning system at field base). The bees were scored every hour, and when individuals completely ceased movement as a result of desiccation, they were recorded. Because of time constraints during the wet season, the desiccation assay was capped at 30 h to maximise the number of individuals tested. Very few individuals made it to the 30 h cap, at which point only 13 of the 172 *B. puangensis* (<10%), and three of the four *C. dentipes* were still alive across all trials, while none of the 195 *H. fijiensis* were alive. Because of the low sample size of *C. dentipes*, we excluded that species from analysis but included it in the figure for comparison.

Metabolic rate

We estimated resting metabolic rate by measuring the rate of carbon dioxide production (\dot{V}_{CO_2} , $\mu\text{l h}^{-1}$) using standard flow-through respirometry techniques with a seven-channel respirometry system (Alton et al., 2017; Lighton, 2018). The respirometry system was supplied with air that was drawn from the room with a 12 V pump and pushed through columns of soda lime and Drierite® to remove CO₂ and water vapour, respectively. The flow of air through each of the seven channels of the system was regulated nominally to 100 ml min⁻¹ by a mass flow controller (model GFC17, Aalborg, Orangeburg, NY, USA). The volumetric flow rate produced by the flow controller was measured using a Gilian Gilibrator-2 NIOSH Primary Standard Air Flow Calibrator with a low-flow cell (Sensidyne, LP, St Petersburg, FL, USA) and corrected to standard temperature and pressure (STP, i.e. 101.3 kPa and 0°C). After the flow controller, the air passed through a humidifying chamber (a syringe of wet cotton) before flowing through a respirometry chamber (2.5 ml plastic syringe) containing an individual bee. The respirometry chamber containing the bee was placed inside a temperature-controlled cabinet that maintained air temperature to 25±1°C and kept bees in the dark. The excurrent air from the respirometry chamber then flowed through one of eight infrared CO₂/H₂O gas analysers (model LI-840A, LI-COR, Lincoln, NE, USA) that measured CO₂ concentration at a sampling rate of 1 Hz, and were calibrated with precision span gases (5.0 and 30.4 ppm CO₂, Alphagaz, Air Liquide, Melbourne, VIC, Australia).

The fractional CO₂ concentration of the excurrent air from each chamber was recorded for 50 min ($F_{E_{CO_2}}$). The fractional CO₂ concentration of the incurrent air with an empty chamber was measured for 2 min before and after each 50 min measurement block (after a 10 min washout period for CO₂ concentration to reach a stable value) and a linear model was fitted to these data to estimate the CO₂ concentration of the incurrent air during the 50 min measurement period ($F_{I_{CO_2}}$). \dot{V}_{CO_2} was then calculated using eqn 1 from Lighton (2018), where FR is the flow rate corrected to STP (i.e. 101.3 kPa and 0°C), accounting for water vapour dilution:

$$\dot{V}_{CO_2} = FR(F_{E_{CO_2}} - F_{I_{CO_2}}). \quad (1)$$

The lowest \dot{V}_{CO_2} averaged over 20 min during the final 35 min of the measurement period was taken as the measure of metabolic rate for each bee. The first 15 min of the measurement period was discarded as it was considered a settling period and this was a sufficient amount of time for the bees to enter a quiescent state as observed by the emergence of discontinuous patterns of gas exchange in more than 98% of bees in the study (discontinuous gas exchange patterns only occur when an animal is in a quiescent state: Kestler, 1985; Lighton, 1998).

We were unable to collect enough *C. dentipes* for this assay and therefore compared metabolic rates of *B. puangensis* and *H. fijiensis* only. Species and sex were measured in a randomised order over a period of 5 days during September.

Mass measurements

As we did not have access to a high-precision balance in the field, individuals were preserved in 100% ethanol immediately following performance measurements. Before the bees were weighed, we detached the right hindleg of each individual for a population genetics barcoding project (data not included in this manuscript). Specimens were then dried at 60°C for 48 h before having their dry mass measured (XP2U Ultra Micro Balance, Mettler Toledo, VIC, Australia).

Statistics

We ran linear models in the statistical program R (<http://www.R-project.org/>) to assess for differences in performance between the endemic and invasive bee species. The full models for each performance assay included species, season, sex and the interaction between species and season as factors, and body mass as a covariate. Season was not included in full chill coma recovery or metabolic rate models as they were only tested in the dry season. Sex was unbalanced in the full model because only female *C. dentipes* are found in Fiji (some *Ceratina* species are known to become parthenogenic under certain environmental circumstances: Daly, 1966). As *C. dentipes* was not included in the metabolic rate or desiccation resistance analysis, we included a two-way interaction between species and sex within the models for those traits. To account for sex being unbalanced in the full model, we conducted species-specific models for each performance assay as well to gain more accurate insights into how sex affects performance within *H. fijiensis* and *B. puangensis*. We also conducted the species-specific analyses to assess seasonal plastic responses in each species. Finally, we provide sex-specific models for each performance measure in Tables S1–S3 to show that our findings are consistent when both sexes are analysed together or separately. Very few *C. dentipes* were collected for desiccation and metabolic rate comparisons, so *C. dentipes* was excluded from these analyses (statistical comparison of *H. fijiensis* and *B. puangensis* only). Body mass, desiccation resistance (hours) and metabolic rate data were \log_{10} -transformed, and chill coma recovery underwent a square root transformation to ensure linear model assumptions were met (CT_{max} data were not transformed). These models were simplified using stepwise backwards elimination using lmerTest version 3.1-2 package (Kuznetsova et al., 2020) based on Akaike's information criterion to arrive at a minimum adequate model, which was used to predict the relationship between performance trait, body mass and season within each species. Significance of fixed effects was tested using a Type-III *F* test in the car package version 3.0-10 (Fox

Table 1. Linear model summary of the effect of species, season, mass and the interaction between species and season on critical thermal maximum with two-tailed *t*-tests

Coefficient	Estimate±s.e.	<i>t</i>	<i>P</i>
Intercept	44.25±0.14	318.0	<0.001
Species (<i>B. puangensis</i>)	3.33±0.18	17.87	<0.001
Species (<i>C. dentipes</i>)	5.74±0.47	12.30	<0.001
Season (dry)	-1.17±0.20	-5.8	<0.001
\log_{10} Mass	0.77±0.45	1.72	0.086
Species (<i>B. puangensis</i>) × season (dry)	1.11±0.29	3.77	0.0002
Species (<i>C. dentipes</i>) × season (dry)	0.12±0.78	0.15	0.882

The model had a residual standard error of 1.35 on 358 degrees of freedom and an R^2 value of 0.70.

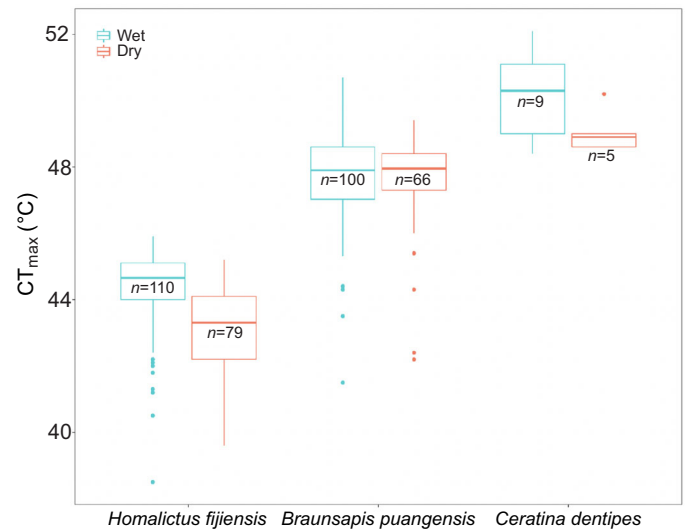


Fig. 2. Critical thermal maximum (CT_{max}) of endemic *H. fijiensis*, and invasive *B. puangensis* and *C. dentipes*. Data are for the wet (April) and dry (September–October) seasons in lowland Fiji.

and Weisberg, 2019). We used the package ggplot2 version 3.3.0 to produce data figures (Wickham, 2011).

RESULTS

CT_{max}

The best-fitting model that explained variation in CT_{max} included a significant two-way interaction between species and season ($F_{2,358}=7.23$, $P<0.001$) and no effect of \log_{10} -transformed mass ($F_{1,358}=2.96$, $P=0.086$) (model coefficient estimates are displayed in Table 1). We found that the invasive bee species, *B. puangensis* and *C. dentipes*, had higher CT_{max} than *H. fijiensis* across the wet and dry season (Fig. 2, Table 1), supporting our hypothesis that invasive bees would have higher thermal maxima than the endemic *H. fijiensis*. *Ceratina dentipes* had the highest mean (\pm s.e.m.) CT_{max} of the three species at $49.74\pm 0.3^\circ\text{C}$, while *B. puangensis* had a mean CT_{max} of $47.7\pm 0.10^\circ\text{C}$, which was 4.18°C greater than the mean CT_{max} of *H. fijiensis* of $43.85\pm 0.32^\circ\text{C}$ (Fig. 2).

Within the species-specific models, we assessed effects of season, body mass and sex on CT_{max} . Within *H. fijiensis*, the best-fitting model that explained the observed variation in CT_{max} included season as a factor, where CT_{max} was higher in the wet season than the dry season (Fig. 2) ($F_{1,183}=36.79$, $P<0.001$). The best-fitting model for *B. puangensis* included \log_{10} -transformed body mass ($F_{1,164}=4.38$, $P=0.038$) as a factor and showed that individuals with greater body mass had slightly higher thermal tolerance. There was no effect of season, sex or \log_{10} -transformed body mass on *C. dentipes* ($P>0.05$). Sex-specific analyses for CT_{max} across all three species are shown in Fig. S1.

Table 2. Linear model summary of the effect that mass and species have on square root-transformed chill coma recovery time with two-tailed *t*-tests

Coefficient	Estimate±s.e.	<i>t</i>	<i>P</i>
Intercept	34.09±1.64	20.86	<0.001
Species (<i>B. puangensis</i>)	3.24±2.20	1.47	0.143
Species (<i>C. dentipes</i>)	-9.67±3.61	-2.66	0.008
Sex (male)	6.67±2.13	3.14	0.002

The model had a residual standard error of 11.23 on 136 degrees of freedom and an R^2 value of 0.16.

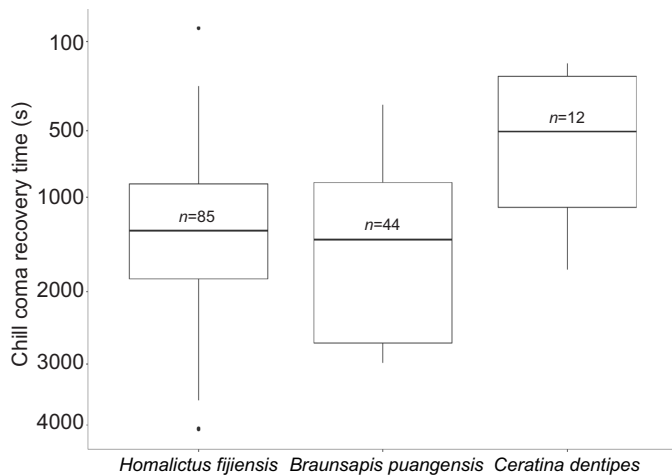


Fig. 3. Square root-transformed chill coma recovery time of endemic *H. fijiensis*, and invasive *B. puangensis* and *C. dentipes*. Data are for the dry (October) season only in lowland Fiji. Faster chill coma recovery times indicate greater cold resistance. The y-axis has been inverted to improve comparison of performance graphs.

Chill coma recovery

The best-fitting model that explained the variance observed in the square root-transformed chill coma recovery data included significant main effects of species ($F_{2,136}=6.26$, $P=0.0025$) and sex ($F_{1,136}=9.83$, $P=0.002$). *Ceratina dentipes* was the most cold resistant with the most rapid chill coma recovery time (mean 697 s) of the three study species (Table 2, Fig. 3), where faster recovery times indicate greater cold resistance. There was no significant difference between chill coma recovery time in *B. puangensis* (mean 1628 s) and *H. fijiensis* (mean 1534 s) (Table 2).

Within the species-specific chill coma recovery models, the best-fitting model for *H. fijiensis* included sex ($F_{1,82}=7.03$, $P=0.009$) as a significant factor. The best-fitting model for *B. puangensis* included \log_{10} -transformed body mass ($F_{1,42}=4.79$, $P=0.034$) as a significant effect. Within the *C. dentipes* model, there was no significant effect of \log_{10} -transformed body mass (sex was not included in models as only females were collected). Sex-specific performance analyses are shown in Fig. S2.

Desiccation

The best-fitting model that described the observed variance in \log_{10} -transformed desiccation resistance included the main effect of species ($F_{1,219}=34.87$, $P<0.001$) as a significant factor, and season ($F_{1,219}=2.59$, $P=0.109$) and sex ($F_{1,219}=3.76$, $P=0.054$) as factors, which did not have statistically significant effects on desiccation resistance. *Braunsapis puangensis* was more resistant to desiccation than *H. fijiensis* (Table 3, Fig. 4), with a mean desiccation resistance of 20 h for *B. puangensis* and 6.7 h for *H. fijiensis*. Although *C. dentipes* was eliminated from the analysis because of the small sample size of four individuals, three of the four had desiccation

Table 3. Linear model summary of the effect of species and season on \log_{10} -transformed desiccation resistance with two-tailed *t*-tests

Coefficient	Estimate \pm s.e.	<i>t</i>	<i>P</i>
Intercept	1.3 \pm 0.05	28.16	<0.001
Species (<i>B. puangensis</i>)	0.40 \pm 0.07	-5.74	<0.001
Season (dry)	-0.11 \pm 0.06	-1.61	0.109
Sex (male)	-0.13 \pm 0.06	-1.94	0.054

The model had a residual standard error of 0.34 on 218 degrees of freedom and an R^2 value of 0.39.

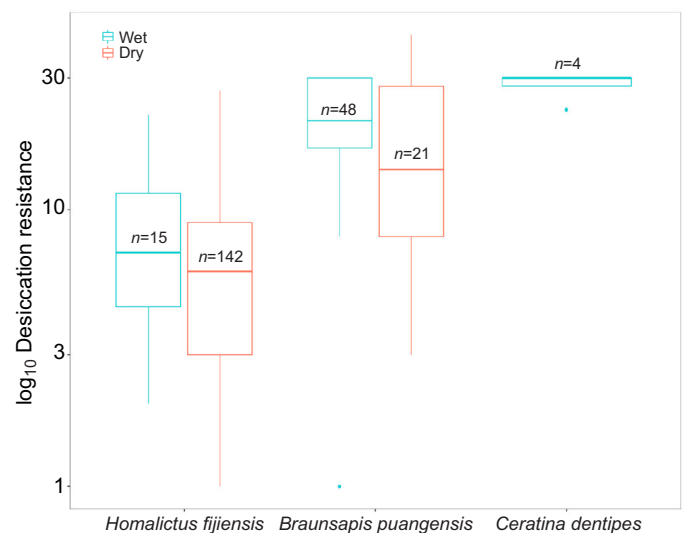


Fig. 4. Desiccation resistance of endemic *H. fijiensis*, and invasive *B. puangensis* and *C. dentipes*. Data are for the wet (April) and dry (September–October) seasons in lowland Fiji. Desiccation resistance (h) was \log_{10} transformed.

resistances over 30 h and the other individual lasted 23 h in the desiccation chamber, and thus we expect they are more resistant to desiccation stress than *H. fijiensis*.

Within the species-specific desiccation resistance models, the best-fitting model for *H. fijiensis* that explained the most variance in desiccation resistance included sex as a factor ($F_{1,154}=3.3$, $P=0.07$), which was not statistically significant. Within the *B. puangensis* model, the best-fitting model that explained the most variance in desiccation resistance included sex ($F_{1,65}=4.64$, $P=0.035$) as a significant factor. Sex-specific analyses are shown in Fig. S3.

Metabolic rate

The minimum adequate model that explained the observed variation in routine metabolic rate included a two-way interaction between species and sex ($F_{1,97}=7.2$, $P=0.008$), and a significant main effect of \log_{10} -transformed body mass ($F_{1,97}=5.32$, $P=0.023$). Within species, male and female *H. fijiensis* had similar mass-independent metabolic rate, while *B. puangensis* females had lower mass-independent metabolic rate than males (Fig. 5). Within females, *H. fijiensis* had higher mass-independent metabolic rate than *B. puangensis*, but the opposite was true in males (Fig. 5).

DISCUSSION

Current hypotheses suggest that invasive alien species are likely to have wider thermal tolerance and higher plasticity than endemic species (Braby and Somero, 2006; Chown et al., 2007; Davidson et al., 2011; Logan et al., 2019; Tepolt and Somero, 2014; Zerebecki and Sorte, 2011). While there is some evidence to support these claims (Forsman, 2015; Janion-Schepers et al., 2018; Liao et al., 2016), more empirical data across a range of systems are required to assess the functional basis for the success of invasive alien species and how functional variation will modulate the effects of climate change on invasive compared with native species (Kelley, 2014). Here, we provide a case study comparing the thermal tolerance, desiccation resistance, metabolic rates and seasonal adjustments of two invasive and one endemic bee species in Fiji. Understanding how both climate change and the threat of invasive alien species will interact to impact ecosystem functioning is critical, particularly in

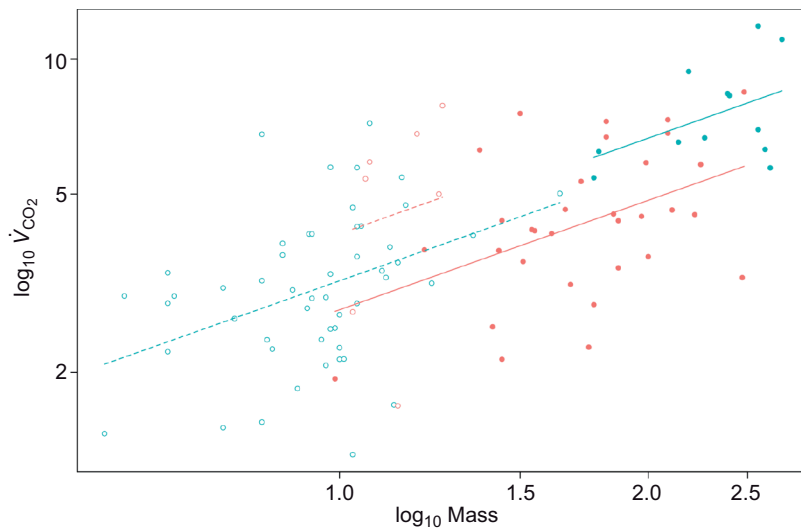


Fig. 5. Relationship between routine metabolic rate and body mass for endemic *H. fijiensis*, and invasive *B. puangensis* and *C. dentipes*. The data show a linear relationship between \log_{10} -transformed routine metabolic rate (measured as the rate of CO_2 production, \dot{V}_{CO_2} , $\mu\text{l h}^{-1}$) and \log_{10} -transformed body mass (g) for endemic bee *H. fijiensis* males (open blue symbols and dashed lines, $n=51$) and females (filled blue symbols and solid lines, $n=12$) and the invasive bee species *B. puangensis* males (open red symbols and dashed lines, $n=7$) and females (filled red symbols and solid lines, $n=32$). The plotted relationships are derived from the parameter estimates (means \pm s.e.) of the minimum adequate model that included \log_{10} mass (parameter estimate: 0.81 ± 0.19 , $t=4.20$, $P<0.001$), species (parameter estimate for *H. fijiensis*: 0.13 ± 0.06 , $t=2.39$, $P=0.01$), sex (parameter estimate for males: 0.17 ± 0.07 , $t=2.30$, $P=0.02$), an interaction term between species and sex (parameter estimate for *H. fijiensis* \times males: -0.24 ± 0.09 , $t=-2.68$, $P=0.008$), and an intercept term (parameter estimate: -2.56 ± 0.05 , $t=-47.76$, $P<0.001$). The model had a residual standard error of 0.15 on 97 degrees of freedom, and an adjusted R^2 value of 0.45.

regions that are highly vulnerable to climate change, such as the South West Pacific.

Performance trends in invasive and endemic bees

We found that the invasive bee species *C. dentipes* had the highest CT_{max} , greatest desiccation resistance and most rapid chill coma recovery time (i.e. it was the most cold tolerant) of the three study species. *Braunsapis puangensis*, the other invasive alien species, was also more tolerant of high temperatures and desiccation than the endemic *H. fijiensis*; however, we found no difference in cold tolerance between *B. puangensis* and the endemic *H. fijiensis*. These findings support our hypothesis that the invasive bee species tend to be more tolerant to stressors than the endemic *H. fijiensis*. The similar cold tolerance between *H. fijiensis* and *B. puangensis* could be due to mild Fijian climates in terms of cold stress, and high cold tolerance may not be a characteristic needed for the successful establishment of an invasive alien species in this region. The R^2 value for the multi-species chill coma recovery model indicated that only 16% of the observed variation in cold tolerance is explained by variation in species and body mass, suggesting that other physiological or behavioural traits might be more important predictors of cold tolerance. Insects are likely to go into a chill coma when they lose their ability to maintain ionic homeostasis, and

thus variation in lipid membrane structure or nerve responsiveness might be a more important predictor of chill coma recovery (MacMillan and Sinclair, 2011).

Seasonal performance

Homalictus fijiensis had a greater ability to shift their CT_{max} between seasons than the invasive alien species, while no species was found to shift desiccation resistance in response to seasons. The lack of seasonal variation observed for desiccation might be explained by limited seasonal change in humidity in Fiji, where mean humidity is 86% in April (wet season) and 83% in September–October (dry season) (<https://www.timeanddate.com/weather/fiji/suva>). Perhaps low variation in seasonal humidity has led to low selection for seasonal adjustment of desiccation resistance. In contrast, latitudinally restricted rainforest *Drosophila* species have high levels of plasticity for desiccation stress (Kellermann et al., 2018), and thus the factors that determine plasticity for certain traits are likely to be more complicated than simply the environmental conditions that a population currently experiences (e.g. evolutionary history, performance breadth and costs of plasticity) (da Silva et al., 2019; DeWitt, 1998; Gabriel, 2005). Although we could not measure plasticity (seasonal acclimation) per se, a lack of seasonal adjustment for desiccation

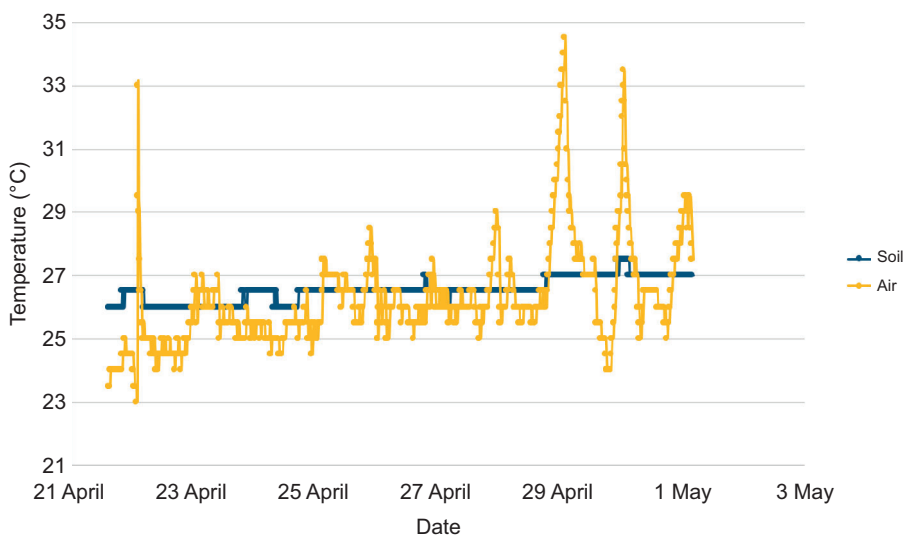


Fig. 6. Thermal variation between nesting environments of endemic *H. fijiensis*, and invasive *B. puangensis* and *C. dentipes*. Thermochron iButton® (<https://thermochron.com.au/>) temperature data showing the difference in thermal variation between measurements taken 30 cm deep into the soil (blue; *H. fijiensis* ground-nesting thermal environment) and 1 m above the ground air temperature (yellow; invasive stem-nesting bee thermal environment) in Suva, Fiji (GPS coordinates: -18.145393 , 178.433104). Data are from April and May 2019.

resistance and larger seasonal shifts in heat resistance for *H. fijiensis* suggests that the invasive alien species are unlikely to be more plastic than *H. fijiensis*. While a meta-analysis by Kelley (2014) suggests invasive alien species have greater acclimation responses to high temperatures than native species, Tomlinson et al. (2015) also found that the native Australian bee species *Amegilla cingulata* had greater acclimation capacity than the introduced *A. mellifera* (European honeybee).

We suggest that the variation in CT_{max} across seasons in *H. fijiensis* could be due to developmental and/or adult acclimation. Because *H. fijiensis* has a narrower thermal tolerance than the invasive *C. dentipes* and *B. puangensis*, seasonal adjustments would allow *H. fijiensis* to maintain performance across seasons. *Braunsapis puangensis* and *C. dentipes* might not require the ability to adjust their CT_{max} with season as their broad thermal tolerance is likely to allow them to maintain performance across daily and seasonal thermal variation in Fiji (see da Silva et al., 2019, for further discussion on the co-evolution of thermal acclimation and thermal tolerance). Many studies have shown across taxa (e.g. copepods, *Drosophila* and aphids) that developmental temperature plays a major role in the upper thermal limits of adults (Gray, 2013; Healy et al., 2019; Kellermann et al., 2017). This could enable *H. fijiensis* populations to shift their upper thermal limits with seasonal change across generations depending on developmental temperature. However, without directly comparing the effects of developmental temperature or adult acclimation capacity for the three study species, it is difficult to determine the driver of the seasonal adjustments in CT_{max} that is observed in *H. fijiensis*.

Metabolic rate of invasive and endemic bees

Homalictus fijiensis females had greater mass-independent routine metabolic rate than male and female *B. puangensis* (but male *B. puangensis* had greater mass-independent routine metabolic rate than male *H. fijiensis*). This result was in contrast to our expectations based on the ‘increased intake hypothesis’, from which the invasive alien species were predicted to have greater mass-independent metabolic rate reflective of a greater energetic expenditure on growth and reproduction (Boratyński and Koteja, 2010; Burton et al., 2011; Lagos et al., 2017; McMahan, 2002). As female bees were most likely in a reproductive state when metabolic rate was estimated (*B. puangensis* and *H. fijiensis* are multivoltine as per field observations), the higher mass-independent metabolic rate observed in *H. fijiensis* females might reflect a greater energetic investment in reproduction than in *B. puangensis*. Alternatively, under a model of energy allocation between maintenance and reproduction (Pettersen et al., 2018), lower metabolic rates observed in *B. puangensis* females could indicate lower maintenance costs than in *H. fijiensis* females, potentially allowing survival through resource scarcity upon entry into a new environment or during dispersal (Burton et al., 2011; Nilsson, 2002). Rising temperatures are generally associated with an increase in maintenance metabolic costs (Clarke and Johnston, 1999; Dillon et al., 2010), meaning that both invasive and endemic species would need to increase foraging activity to obtain more energetic resources to cover the increased cost of self-maintenance at higher temperatures. Competition for floral resources (*H. fijiensis* and *B. puangensis* are known to exhibit partial floral overlap; da Silva et al., 2016; Crichton et al., 2019) between the two species could therefore increase in a warming climate scenario. Hence, greater energetic demands, and narrower foraging windows associated with low upper thermal tolerance, could impact on allocation to maintenance and reproduction in *H. fijiensis* populations, potentially increasing their vulnerability to climate change.

Nesting ecology effects on invasiveness and thermal performance

Both of the invasive alien species in our study, *B. puangensis* and *C. dentipes*, are stem-nesting bees which experience greater daily environmental thermal variability in their nests than the endemic ground-nesting *H. fijiensis* (Fig. 6). This is because underground environments are more buffered against ambient temperature fluctuations than nests in dead stems. This might explain why the two invasive alien species have broad thermal tolerance with little apparent adjustment of their upper thermal limits between seasons. Potentially, *H. fijiensis* does not need to be as heat resistant as the two invasive alien stem-nesting species because they can hide within their cooler ground nests during extreme temperatures, which might buffer them from a warming climate. However, hiding within nests during hot temperatures is a short-term solution to climate change, and more frequent hiding behaviour is likely to reduce their daily foraging windows. A review of invasive bee species around the world shows that 69% of invasive bees live in stems or existing cavities or bore into wood (Russo, 2016). Stem-nesting insects are easily introduced into new regions via the trade in ornamental plants, and therefore their degree of invasiveness is also probably attributed to the ease of nesting substrate transport. Regardless of whether stem-nesting bees are invasive as a result of their broad thermal tolerance or assisted dispersal, their broad thermal tolerance is likely to assist in their settlement and success in new habitats.

Concluding remarks

We found that the invasive bee species, *C. dentipes* and *B. puangensis*, in lowland Fiji are more heat and desiccation tolerant and have reduced energetic demands than the endemic *H. fijiensis*. These characteristics indicate that the invasive alien species are more likely to be resilient to rising temperatures and reduced foraging opportunities than *H. fijiensis*, and therefore are likely to cope better with future climate change in Fiji. We found no evidence that seasonal adjustments were larger in invasive alien species, but instead high thermal tolerance annually is likely to ensure they are more robust to global warming than *H. fijiensis*.

Lastly, it is important to consider whether the differing climatic tolerance of the invasive and endemic bee species examined here will change plant–bee pollination networks in a warming future. The foraging behaviour of *C. dentipes* has not been studied, and although *B. puangensis* is a generalist forager, its host-plant breadth is not nearly as great as that of *H. fijiensis* (Crichton et al., 2019; Draper et al., 2021). Hence, climate-related loss of *H. fijiensis* might have serious implications for lowland Fijian pollination networks. In future studies, the resilience of natural and agricultural pollination services should be examined as the loss of the supergeneralist *H. fijiensis* might have a disproportionate impact compared with the loss of the invasive alien species.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

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M.C.E., S.G., M.T., M.I.S., L.A.A., M.P.S., V.K.; Visualization: C.R.B.d.S., M.C.E., V.K.; Supervision: C.R.B.d.S., S.G., M.T., M.P.S., V.K.; Project administration: C.R.B.d.S., M.P.S.; Funding acquisition: C.R.B.d.S., M.I.S., L.A.A., M.P.S., V.K.

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Data availability

Data are available from the Monash University figshare data repository: <https://doi.org/10.26180/13347173>

Supplementary information

Supplementary information available online at <https://jeb.biologists.org/lookup/doi/10.1242/jeb.230326.supplemental>

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