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ORIGINAL ARTICLE

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Against the odds: Nesting specialization and foraging ecology provide insights into climate change responses in a mountain bee

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Abstract

1. Climate change is rapidly altering temperature regimes in mountain environments, reshaping the distribution and activity of pollinators. Studies of insect pollinator assemblages in mountains show a general pattern of decreasing bee (Anthophila) activity with increasing elevation.
2. Here we report a unique *Exoneura* bee, that counters this trend and thrives in cold, high-elevation (~1500–1900 m a.s.l.) woodlands at the tree line. While other members of the genus at lower elevations nest in narrow pithy or hollow plant stems, this bee has a unique nesting biology, burrowing into the dead branches of the only tree in Australia's subalpine zone (snow gum, *Eucalyptus pauciflora* subsp. *niphophila*).
3. Using a combination of observational surveys, spatial mapping, temperature tolerance tests and biophysical modelling, we investigated various aspects of the bee's ecology. We found that this species' nest abundance peaked at the tree line (approx. 1900 m m a.s.l). Foraging behaviour was highly dependent on the presence of snow gums for nesting, with activity concentrated within 30 m of snow gum stands.
4. Biophysical modelling showed that the daily and annual foraging activity window was significantly limited by temperature and that it will substantially increase under climate change projections.
5. This study reveals several unique traits of a new bee species that show a close association with snow gums, providing insights into its flourishing in the changing conditions of subalpine Australia's high-elevation environments.

KEYWORDS
climate change, *Exoneura*, foraging behaviour, pollinator activity, snow gum

INTRODUCTION

In mountain ecosystems, climate change is driving some of the earliest and most pronounced shifts in abiotic conditions (Pickering & Buckley, 2003), with impacts recorded on mountain pollinator communities (Buckley & Kingsolver, 2012; Inouye, 2020). Abiotic factors impact pollinators' activity levels, thermoregulation, phenology and mortality (Hoiss et al., 2015). As a result, pollinator communities in high-elevation environments are often compositionally distinctive (Coates et al., 2024), such as the reduced diversity of bees (Apoidea)

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in high-elevation pollinator communities, where they are replaced by flies (Diptera) (McCabe & Cobb, 2021). Because pollinators differ in their capacity to transport and deposit pollen effectively, variation in pollinator community composition can strongly influence plant reproductive success and community structure (Herrera, 1987). Given that insect pollinators are ectotherms, it is essential to understand the thermal sensitivity underpinning their foraging activity in order to predict how climate change may alter pollination dynamics in these vulnerable environments.

Insect pollinators persist in cold environments due to a combination of behavioural and physiological traits that allow them to maintain foraging activity. For instance, *Bombus* bees, important alpine pollinators in the northern hemisphere, display both behavioural (e.g., vibrating flight muscles to generate warmth) and physiological traits (e.g., insulation via dense setae, large body size for increased thermal mass) that allow them to forage in the cold (Heinrich, 2004; Minachilis et al., 2020). Other bee species rely on their nesting site to provide passive thermal insulation from ambient temperatures (Antoine & Forrest, 2021; Jones & Oldroyd, 2006). These traits allow pollinators to maintain thermally suitable conditions required for flight and foraging activity.

By coupling climate data with information on species' traits and thermal activity thresholds, such as through using biophysical modelling approaches, we can predict how climate warming will alter the daily or seasonal duration available for essential behaviours like foraging (Briscoe et al., 2023). For instance, Buckley and Kingsolver (2012) use biophysical modelling to show how the available flight time for *Colias* butterflies declined for species at a warmer, lower-elevation site, but increased for species in colder, high-elevation sites. Biophysical modelling has also been used to assess how vertebrate ectotherms' activity time will shift under climate change (Gao et al., 2024; Kearney et al., 2008; Muñoz et al., 2022), with Gao et al. (2024), demonstrating greater increases in activity time for lizards at higher elevation sites.

Australia's unique biogeographic history means that its bee fauna is distinct, accounting for approximately 10% of global bee species richness (Michener, 2007). Australia is home to endemic taxa such as the family Stenotritidae, an unusually high proportion of species in the family Colletidae, Euryglossinae (Michener, 2007) and the genus *Exoneura* (Schwarz et al., 2006). On the other hand, several taxa with widespread global distributions, such as Andrenidae, Mellitidae, *Apis* and *Bombus*, are not found natively in Australia (Batley & Hogendoorn, 2009). Whereas the cold-tolerant *Bombus* species are often abundant at high elevations elsewhere in the world (Minachilis et al., 2020), Coates et al. (2024) showed that *Exoneura* were the only abundant bee in subalpine Australian woodlands.

Exoneura is an endemic Australian stem-nesting bee genus (Cronin & Schwarz, 1999a), representing 67 of the 197 Australian Apidae species (Batley & Hogendoorn, 2009; Michener, 1965). Due to their facultatively social behaviour, the genus has been the focus of several studies on the evolution of sociality in insects (Bernauer et al., 2021; Michener, 1965; Schwarz, 1986; Schwarz & O'Keefe, 1991). *Exoneura* are typically stem nesters, excavating burrows into exposed pithy plant stems, such as in native *Dicksonia* tree ferns and in *Rubus* stems (Coates et al., 2022; Schwarz, 1986). Researchers have suggested that *Exoneura* are incapable of burrowing into hard materials due to their small mandibles and weak musculature (Rayment, 1951; Silberbauer & Schwarz, 1995), although *E. robusta* Cockerell has been observed nesting in rotting *Eucalyptus* wood (Cronin & Schwarz, 1999b). Because they exhibit little morphological variation, *Exoneura* are difficult to identify to species, and while it has long been recognized that the genus requires taxonomic revision (Schwarz et al., 1996), the taxonomy remains poorly resolved. Genetic sequencing by Takeshima et al. (in prep) indicates that the *Exoneura* present in subalpine woodlands cluster closely with *E. bicolor* Smith, but may represent an undescribed species. Accordingly, we refer to *Exoneura* present in our study area as *E.* cf. *bicolor*, reflecting their unresolved taxonomy. In other studies, *E. bicolor* primarily nests within pithy plant stems (Cane & Michener, 1983; Schwarz, 1986; Schwarz & O'Keefe, 1991; Silberbauer & Schwarz, 1995), with some anecdotes also noting occasional nesting in decaying *Eucalyptus* branches (Silberbauer, 1992; Silberbauer & Schwarz, 1995), and opportunistic use of holes bored in wood by beetles (Michener, 1965; Rayment, 1951).

In this study, we examine the unique traits of *E.* cf. *bicolor* in the subalpine woodlands of Australia's highest mountains. We investigate the behavioural and physiological traits that enable this subalpine bee to thrive in cold, high-elevation habitats and use these traits to make predictions about their response to climate change. In our subalpine study area, we have observed *E.* cf. *bicolor* burrowing within large woody branches and trunks of dead snow gum (*Eucalyptus pauciflora* subsp. *niphophila* (Maiden & Blakely) L. A. S. Johnson & Blaxell), progressively excavating nests over a period of days. This nesting habit is unusual among other stem-nesting *Exoneura*, which are often considered incapable of burrowing into wood (Rayment, 1951; Silberbauer & Schwarz, 1995). We examine the role that the bees' unique nesting substrate plays in shaping their abundance at elevation and foraging activity. We also quantify the bees' thermal activity window and thermal tolerance limits to parameterize biophysical models, which we use to quantify the bees' annual activity window and forecast how that will be affected by climate warming.

METHODS

Study sites

We conducted fieldwork in Kosciuszko National Park, New South Wales, Australia from November 2022 to February 2023. Previous work by Coates et al. (2024) indicates that this period captures *E.* cf. *bicolor*'s activity period in the subalpine zone, which also coincides with the onset of peak flowering (Costin et al., 2000). Most of our sampling was conducted at Charlotte Pass (~1850 m a.s.l., 36° 25′ 55.5672″ S, 148° 19′ 44.076″ E), where we surveyed nest activity, foraging distances and collected bees for thermal assays. An additional site, downslope at Perisher (~1720 m a.s.l., 36° 24′ 16.1″ S, 148° 24′

50.0″ E), was also sampled for nest activity, and the nest survey extended down to Sawpit Creek at 1400 m a.s.l.

Nest abundance with elevation

To determine the elevational extent of subalpine *E.* cf. *bicolor* populations, we surveyed dead *Eucalyptus* branches for nest entrances, sampling along an elevational gradient. Sites were located from approximately 1400 to 2000 m a.s.l. along Kosciuszko Road. Several other *Eucalyptus* species are found in montane forests at the bottom of this gradient, including *E. dalrympleana* Maiden, *E. camphora* Baker and *E. stellulata* Sieber, while from ~1600 m a.s.l., only snow gums are present (Duncan & McDougall, 2010). We determined 1400 m a.s.l. as the lower bound for the survey after no nests were found below 1530 m. To select sample sites, we examined this gradient in seven bands each covering 100 m of elevation and calculated the horizontal extent within each elevation band along the main road in the park. We used a random number generator to select three sites to sample within each elevation band for a total of 21 sites (Table S1).

At each site, we walked both north and south on either side of the road until we reached a *Eucalyptus* stand, where we surveyed the first 20 suitable branches for the occurrence of nest entrances. Initial observations of nest sites indicated that only dead branches that were free of bark and at least 10 cm in diameter were colonized, so only these were included as suitable branches in the survey. We also did not survey branches that were difficult to access, above 2 m in height. Nest entrances were defined as those where either an *E.* cf. *bicolor* individual could be seen within the nest or where the characteristic rim created by the species during nest excavation was visible at the nest entrance (Figure S1).

Foraging and canopy cover

To determine how *E.* cf. *bicolor* foraging behaviour relates to the presence of snow gum nesting sites, we conducted pollinator visitation surveys along transects with increasing distance from snow gum stands. We established seven transects near Charlotte Pass, ensuring a spread of aspects and slope gradients (upslope, downslope and cross-slope). We ensured that snow gum stands nearby to plots had dead snow gum branches with active *E.* cf. *bicolor* nests. In each transect we conducted sampling at three plots along increments (near, middle, far) leading away from snow gum stands. Plots were circular, with a 30 m radius. We conducted consecutive 20-min surveys, one at each of the three plots, where we recorded all visits of *E.* cf. *bicolor* to flowers, recording a visit when the reproductive parts of a flower were contacted.

We analysed the spatial relationship between trees and foraging locations using Geographic Information System (GIS) mapping. We obtained high-resolution LiDAR (Light Detection and Ranging) point cloud data for the study area collected via an ALS50 (SN092) sensor (Geoscience Australia, 2023). These data were pre-processed to ICSM Classification Level 3 (Intergovernmental Committee on Surveying and Mapping, 2008), whereby ground return (bare earth) and non-ground return (e.g., vegetation, buildings) data points are distinguished, which enabled us to determine canopy cover within the study area.

Using the LAS toolbox in ArcGIS Pro 3.1.3 (Esri Inc., 2023), we initially processed the LiDAR data into LAS format using the *Convert LAS* tool. Using the *Make LAS Dataset Layer* tool, we filtered out LAS data points according to the LAS 1.3 standard (The American Society for Photogrammetry & Remote Sensing, 2010) to create a dataset containing only LiDAR Point Classes 4 (Medium vegetation) and 5 (High Vegetation). We visually inspected this dataset by overlaying satellite imagery to ensure that only snow gum canopy was captured within this output raster. We then rasterized, standardized and inverted this data to create a raster containing values of 1 where snow gum canopy is present and values of 0 where absent. Finally, this raster was converted to a vector layer containing only snow gum canopy cover.

We then quantified the proportion of canopy cover within a radius distance of each plot by creating circular buffers around each plot using the *Buffer* tool. We created 10 different sized buffers (10–100 m radius) to determine the distance from snow gum canopy that best predicted *E.* cf. *bicolor* abundance. Finally, we used the *Tabulate Intersection* tool to quantify the overlap (in m^2) of snow gum canopy cover within each circular buffer.

Activity at the nest

To monitor the effect of temperature on activity at the nest entrance, we placed camera traps with iButton temperature loggers at *E.* cf. *bicolor* nest entrances at Perisher and Charlotte Pass. We built five camera traps following Droissart et al. (2021), which consisted of a Raspberry Pi Zero W microcomputer, Raspberry Pi infrared camera module with a 2.6 mm 5MP lens, a 30,000mAh battery pack, a 128 GB SD card and a waterproof case. Each camera trap was paired with two iButton temperature loggers placed within a Stevenson screen, which monitored ambient air temperature every 5 min at a height of 1.2 m. Video files and iButton temperature logger timestamps were synchronized, so that we could pair ambient temperature with activity. We mounted cameras on poles placed ~15–20 cm from nest entrances, positioned so that their shadow did not fall across the nest entrance. Cameras were set to record continuously from 6 am until 8 pm, capturing the full window of potential activity from this diurnal species. Cameras captured consecutive one-hour-long videos until the battery discharged, usually after 3–5 days of recording. We then collected the cameras and recharged them overnight, redeploying them the next day.

We processed video files after each camera was collected from the field following Droissart et al. (2021). Similar ex situ motion detection methods have previously been shown to be effective in detecting pollinator movement (Azarcoya-Cabiedes et al., 2014; Weinstein, 2015). We processed videos with DVR-Scan software (Castellano, 2025) to filter out motion sequences. Initially, we

determined the ideal threshold for motion detection by incrementally adjusting the motion detection threshold using video files that contained *E.* cf. *bicolor* activity. This allowed us to reduce the possibility of false negatives while limiting review time created by false positive detections, such as those triggered by movement from wind, rain or snow (Weinstein, 2015).

We manually reviewed motion-sequenced video files to record the occurrence of *E.* cf. *bicolor* activity. When possible, we determined the foraging trip time when only one bee was recorded arriving and departing, without interruption from another bee accessing the nest entrance in the intervening period.

Critical thermal limits

To determine the critical thermal limits of *E.* cf. *bicolor*, we collected individuals by hand netting from flowers. We then transported them to the lab within 3 h to conduct thermal assays. Bees were placed into individual 55 × 20 mm plastic dram vials with air holes in the lid and fluon coating the interior walls to prevent them from climbing away from the heat source. We placed the vials within holes milled into a high-density foam block to insulate against ambient temperature, with the bottom of each vial contacting a Peltier plate. We used a thermoelectric Peltier plate (Model Number CP-121HT, TE Technology, INC.) attached to a controller (Model Number TC-720, TE Technology, Inc.). To record the temperature experienced by bees within each vial, we used K-type thermocouple loggers (DT-847U, Instrument Choice) placed within empty vials alongside the vials containing bees.

For each experimental run, we placed up to 14 bees in an array of vials. We held bees at 22°C for 10 min, before ramping down to −10°C at a rate of 0.25°C/min. We monitored bees continuously for signs that they had reached their lower thermal limits (CT_{min}). CT_{min} was defined as the point at which an individual is no longer able to right itself after being flipped on its back (Kingsolver & Umbanhowar, 2018). We then allowed the bees to cool further, until they ceased all movement and entered a chill coma (MacMillan & Sinclair, 2011). We removed the bees from the Peltier plate following the chill coma and allowed them to equilibrate at room temperature. We then immediately began upper thermal limit (CT_{max}) trials, by returning bees to the Peltier plate and holding them at 22°C for 10 min, before ramping to 60°C at a rate of 0.25°C/min. We observed bees continuously for signs of CT_{max}. CT_{max} was defined as the onset of involuntary muscular spasms, which is commonly used as an upper temperature threshold for ectotherms (Lutterschmidt & Hutchison, 1997; Oyen & Dillon, 2018). Finally, heat death temperature was also recorded, determined by cessation of movement.

Analysis

We conducted all analyses within R Studio Version 4.2.2 (R Core Team, 2022). To determine the influence of elevation on *E.* cf. *bicolor* nest abundance, we constructed a generalized linear model using the *glm.nb* function in the 'MASS' package (Venables & Ripley, 2002) and used a negative binomial model due to the presence of over-dispersed count data. We checked statistical significance using the *summary* function and performed model validation using the *check_model* function within the 'performance' package (Lüdecke et al., 2021).

To analyse the relationship between *E.* cf. *bicolor* abundance and canopy cover within each circular buffer at each plot, we developed zero-inflated negative binomial models incorporating canopy cover as a conditional variable to account for zero inflation. The analysis was performed using the *zeroinfl* function from the 'pscl' package (Jackman, 2024), specifying a negative binomial distribution for the count data and a logit link function for the zero-inflation model component. To evaluate each model's fit and compare it against a simpler model without zero inflation, we employed the Vuong's closeness test, using the *vuong.test* function in the 'mpath' package (Wang, 2024). We assessed model diagnostics to ensure the robustness and appropriateness of each model's fit. Pearson residuals were extracted using the *resid* function in the 'stats' package (R Core Team, 2022), specifically tailored for zero-inflated models. We plotted the predicted values against the residuals for visual inspection of patterns that might indicate deviations from model assumptions.

To determine which sized buffer best predicts *E.* cf. *bicolor* abundance, we constructed a series of zero-inflated negative binomial models corresponding to different distances ranging from 10 meters to 100 meters. Model selection was conducted using the *aictab* function from the 'AICcmodavg' package (Mazerolle, 2023).

To analyse the effect of temperature on *E.* cf. *bicolor* activity, we constructed a generalized linear mixed model (GLMM) using the *glmmTMB* function in the 'glmmTMB' package (Brooks et al., 2017). We used a binomial distribution with nest activity as the response variable, with fixed effects for temperature and its quadratic term, as well as an interaction term between site and temperature to assess potential differences between Perisher and Charlotte Pass. To address time autocorrelation within each observation day, we aggregated the data into 30-min intervals and used an autoregressive AR(1) function within model specification (Harrison, 2021; Kristensen & McGillycuddy, 2024). We set time as a factor with explicit levels, grouped by date as a grouping variable using the 'lubridate' package (Grolemund & Wickham, 2011). We included a random effect for Date and Nest ID to account for variation among nests. We performed model diagnostics using the *check_model* function in the 'performance' package (Lüdecke et al., 2021).

To determine the influence of temperature on foraging trip length, we constructed a GLMM with foraging time as the response variable and average, minimum and maximum temperature during the foraging trip as the predictor variables, with Nest ID as a random effect. To test for a difference in the temperature at which bees depart from or return to the nest, we conducted a two-sample *t*-test.

We created mechanistic niche models at each of our two study sites that predict *E.* cf. *bicolor* activity using the 'NicheMapR' package (Kearney & Porter, 2020), parameterizing models using field-collected data (Table S2). These models integrate a species' biological attributes (physiology, behaviour and morphology) with abiotic conditions

(topography, locality, climate) to model biophysical traits such as activity time (Kearney & Porter, 2020). We used the *micro_silo* function to produce hourly estimates of microclimatic conditions during our study period at Charlotte Pass (148.323187, −36.443593; 1850 m a.s.l.), where the species was most abundant according to our sampling and where our camera traps were set up. This function downloads climate data collected from the Australian Government's SILO database, which uses Bureau of Meteorology observational data spatially interpolated to create a gridded raster for our study site during the observation period (Jeffrey et al., 2001).

We then parameterized the *ectotherm* function using physiological traits sampled from individuals collected in the field. Because air temperature is typically coupled with body temperature for small insects (Stevenson, 1985), we treated air temperature sampled from our iButtons as insect body temperature. To avoid the influence of outliers, we used the 1st percentile of activity temperature (15.75°C) recorded from camera traps for minimum foraging temperature (TF_{min}). Because this species is limited primarily by cold conditions, temperatures recorded in the field were not indicative of maximum foraging temperature (TF_{max}) or preferred body temperature (T_{pref}). For example, the maximum temperature we recorded was 28°C, while Jaboor et al. (2022) showed that the maximum foraging temperature for *E. robusta* was 38.82°C. We used the value of 38.82°C for TF_{max}, but it did not influence model outcomes as the study site never approached this temperature. We saw no evidence of basking at nest entrances prior to departing for foraging, so the minimum basking temperature (TB_{min}) was not considered.

We performed Pearson correlation analyses using the *cor.test* function in the 'stats' package (R Core Team, 2022) to validate modelled microclimate and nest activity versus data observed in the field for our sample dates. At Charlotte Pass, modelled microclimate ($r = 0.93$, $p < 0.01$, Figure S2) and activity ($r = 0.74$, $p < 0.01$) were strongly positively correlated with observations, indicating that the model predicted microclimate and nest activity well. However, at Perisher, while the modelled microclimate accurately predicted temperature ($r = 0.88$, $p < 00.1$) activity was only moderately correlated with observed data ($r = 0.66$, $p < 00.1$), indicating a weaker relationship between model predictions and observed nest activity. Because model validation indicated a strong relationship between modelled and observed data at Charlotte Pass but not Perisher, subsequent climate change predictions were only performed at Charlotte Pass, where our field data also indicated the bee is most abundant.

To predict shifts under climate change scenarios, we compared annual foraging activity under present climate conditions to two climate change scenarios in 2100 (Gao et al., 2024; Mi et al., 2022; Muñoz et al., 2022). We averaged activity over 10 years of SILO climate data (2015–2024) to represent the present climate. Representative Concentration Pathway (RCP) 4.5 represents a moderate climate change scenario where greenhouse gas emissions peak around 2040 and then decline, leading to a predicted global average temperature increase of 2–3°C. RCP 8.5 represents a severe scenario where emissions continue unabated and the predicted global average temperature may increase by 4.3–6.1°C (Muñoz et al., 2022). To model these scenarios, we set the warm parameter within *micro_silo* to 2.5°C for RCP4.5 and 5.2°C for RCP8.5 (Gao et al., 2024), thereby projecting future climates for this site that use the same 10 year baseline.

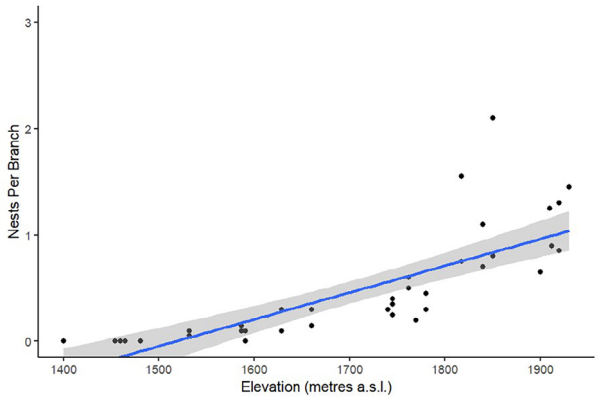


FIGURE 1 *Exoneura* cf. *bicolor* nest abundance per branch across elevation, from a sample of 20 branches at each site. Grey band shows 95% confidence interval.

RESULTS

Nest abundance with elevation

Across 21 sites, we sampled a total of 840 *Eucalyptus* branches, which contained 372 *E.* cf. *bicolor* nests. Nest abundance per branch range from 0 to 2.1 (mean = 0.56 ± 0.51). Nests were only found in snow gum (*E. pauciflora* subsp. *niphophila*) branches, with no nests found in other *Eucalyptus* species at lower sites. No nests were found below 1530 m a.s.l. There was a statistically significant effect of elevation on nest abundance ($p < 0.05$), with an increase in nest abundance observed with increasing elevation (Figure 1).

Foraging and canopy cover

Having considered buffer sizes ranging from 10 to 100 m, model comparison revealed that the model with a 30 m buffer best explained the variation in *E.* cf. *bicolor* abundance with proximity to nearby canopy cover ($AIC_c = 252.05$, $\Delta AIC_c > 2$, Table S3). The functional relationship was positive, with *E.* cf. *bicolor* activity increasing with snow gum canopy cover within 30 m, with very low activity when canopy cover is below 3% (Figure 2).

Activity at the nest

We captured 1287 h of footage across 50 days, in which 825 separate instances of *E.* cf. *bicolor* activity were observed from 16 different nest entrances. In several instances, we observed multiple adults inhabiting the same nest. The range of temperatures captured was −4.5

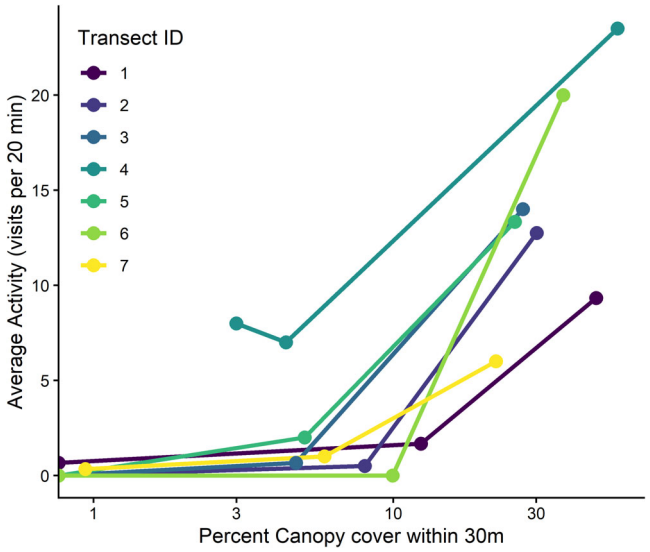


FIGURE 2 The effect of snow gum (*Eucalyptus pauciflora* subsp. *niphophila*) canopy cover on *Exoneura* cf. *bicolor* visitation rate within a 30 m buffer. The grey band shows a 95% confidence interval. Each line displays data from one of the seven transects, with three points showing far, mid and near plots, from left to right.

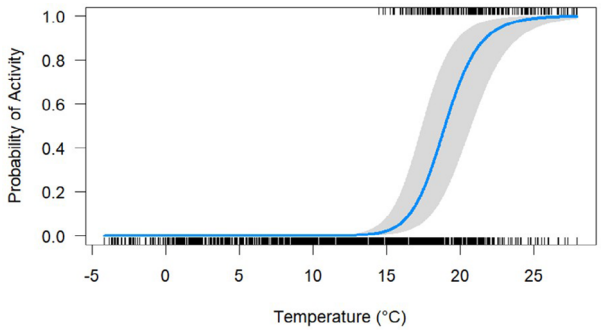


FIGURE 3 Binomial plot showing the effect of temperature on the probability of *Exoneura* cf. *bicolor* activity. The grey band shows ± one standard error. Vertical bars along the top and bottom of the plots show individual observations for the presence and absence of activity, respectively.

to 28°C, with *E.* cf. *bicolor* active above 14.5°C. Activity increased with temperature and became most likely at ~17°C (Figure 3). We did not detect an upper temperature threshold, with activity continuing up to the maximum recorded temperature of 28°C. There was a significant effect of both temperature and the quadratic term for temperature on *E.* cf. *bicolor* activity ($p < 0.05$). Site and the interaction between site and temperature were not significant, indicating no difference between the temperature response for populations at the two study sites. We found no difference between nest departure temperatures and arrival temperatures (paired *t*, $t(289) = 0.31766$, $p > 0.05$).

We were able to determine trip duration on 81 separate foraging trips. Trips ranged from 5 to 90 min, with a mean trip duration of 27.3 ± 16.9 min. We found no significant effect of minimum, maximum or average temperature during the foraging trip on foraging trip duration ($p > 0.05$).

Thermal limits and biophysical modelling of activity

We collected 51 female *E.* cf. *bicolor* individuals for thermal assays: 34 from Charlotte Pass and 16 from Perisher. CT_{min} occurred at 3.5 ± 2.1°C (range 0–7.2°C). Chill coma occurred at −0.16 ± 1.8°C (range −3.3 to 4.6°C). CT_{max} occurred at 44.6 ± 2.9°C (range 37.7–51.6°C). Heat death occurred at 47.1 ± 2.7°C (range 37.7–52.8°C). *t*-tests (Table S4) found no statistical significance of the sampling site on chill coma, CTmax or heat death (all $p > 0.05$), while CT_{min} varied between sites ($p < 0.05$). Thresholds from Charlotte Pass bees were then used to parameterize our biophysical models for this site. No evidence of heterothermic behaviour, such as warming the body through vibrating flight muscles, was observed during assays.

Under present climate parameters, predicted foraging activity at Charlotte Pass spanned from November to March, peaking in January and February, with 89.1 days and 552.7 h of annual activity available. Under RCP4.5, foraging activity increased to 132.6 days and 964.6 h, representing a 48.8% increase in active days and a 74.5% increase in active hours. Under RCP8.5, activity rose further to 172.7 days and 1492.1 h, representing a 93.9% increase in active days and a 170.0% increase in active hours (Figure 4).

DISCUSSION

Here we investigate the ecology of a bee species that manages to survive in Australia's coldest environments, representing a unique cold-tolerant Australian bee. We show that the traits that allow *E.* cf. *bicolor* to thrive in cold climates are unique from the strategies that allow other well-studied cold-tolerant bees, such as *Bombus* (Oyen & Dillon, 2018), to persist in cold mountain environments. By documenting features of *E.* cf. *bicolor*'s nesting, foraging behaviour and thermal ecology, we show that despite physiological constraints that limit the availability of foraging activity, their nesting strategy may offset some of the metabolic costs and temperature thresholds that restrict pollinator activity in mountain ecosystems. However, our findings also highlight vulnerabilities under climate change.

Wood nesting strategy

We have documented that *E.* cf. *bicolor* have shifted to wood nesting from the typical stem nesting habit displayed by other *Exoneura* (Michener, 2007), and suggest that this behaviour has enabled this bee to persist in cold, high-elevation locations where they benefit from reduced competition for floral resources from other bees, but may still face competition from other insects such as flies and moths. The elevational distribution of *E.* cf. *bicolor* nests in our study, with no nests found below 1530 m a.s.l., closely mirrors the elevational

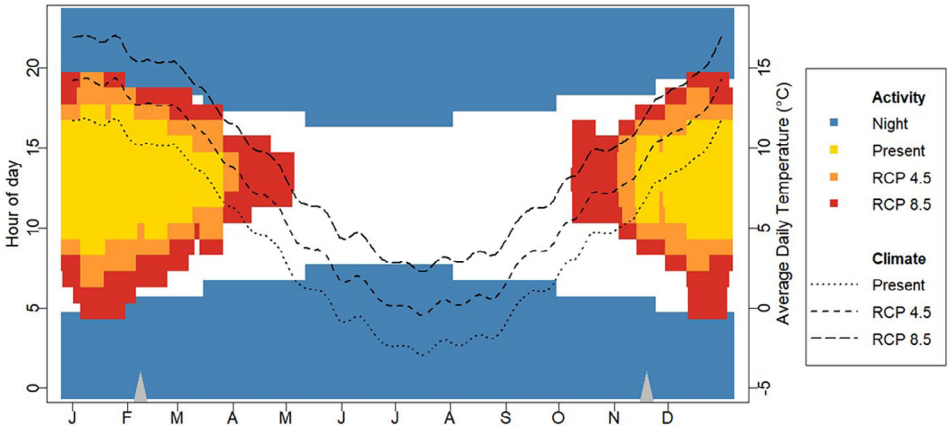


FIGURE 4 Predicted annual activity period for *Exoneura* cf. *bicolor* at Charlotte Pass, shown for present climate, RCP 4.5 and RCP 8.5 climate scenarios. Lines indicate average daily temperature, with axis on right. Grey triangles on bottom axis indicate the field data collection period (November to February).

distribution of snow gums, which are the only trees above 1600 m a.s.l. (Duncan & McDougall, 2010). Wood as a nesting substrate provides important thermal insulation benefits, buffering nest temperatures from cold ambient conditions (Jones & Oldroyd, 2006). Nesting in wood is likely to be thermally advantageous in this environment relative to soil-nesting or stem nesting. Beyond thermoregulation, wood cavities are longer-lived than stems, enabling multi-season persistence and natal nest reuse by daughters (Silberbauer & Schwarz, 1995). Takeshima et al. (in prep) showed that *E.* cf. *bicolor* were present on flowers down to 900 m a.s.l. near our study area, even though we found no nests in wood below 1530 m a.s.l. in our survey. It is unclear whether the *E.* cf. *bicolor* collected at lower sites nearby (Takeshima et al., in prep) nest in wood or stems. Importantly it is also yet to be determined whether the populations of this newly discovered bee are interbreeding or discontinuous.

Evidence for the relatively low competition for floral resources at higher elevations comes from surveys of flower visitors in these sites (Coates et al., 2024; Inouye & Pyke, 1988). Coates et al. (2024) showed that at Charlotte Pass, *Exoneura* comprised 71% of visits from bees to flowers, representing a higher proportion than for *Exoneura* at lower-elevation sites along an elevational gradient down to 900 m a.s.l, where *Exoneura* comprised 38% of bee visits. This study also showed that bees tended to visit different plant families than flies, which were most abundant at high-elevation sites, so that resource partitioning may allow for reduced floral competition between flies and *E.* cf. *bicolor* at these sites (Coates et al., 2024).

Foraging opportunities

Given that *E.* cf. *bicolor* restricts foraging activity to temperatures above 15.75°C, there are limited opportunities for thermally suitable foraging conditions in this environment. As central place foragers with a fixed nesting site, *E.* cf. *bicolor* is unable to move to track suitable microclimatic conditions (Kenna et al., 2021). During our observations from November to February, inclement weather was common, with temperatures failing to surpass 15.75°C for a total of 14 days, including a period of seven consecutive days where no activity was recorded. This contrasts with flies, the most abundant pollinator in this system, which Coates et al. (2024) showed were able to forage at lower temperatures. Other cold-adapted bees, such as *Bombus*, can forage at temperatures as low as 5–10°C (Corbet et al., 1993), while *E.* cf. *bicolor*'s thermal physiology restricts foraging opportunities in this environment.

While bees of this body size are typically capable of flying up to 1 km (Greenleaf et al., 2007), *E.* cf. *bicolor* were primarily foraging within 30 m of nests in areas around snow gum stands. Optimal foraging theory proposes that animals will maximize their net energy gain by balancing the costs of foraging with the energetic value of the resources obtained (Stephens & Krebs, 1986). The fact that *E.* cf. *bicolor* achieve a net energy gain foraging in such a small area, and in only limited suitable foraging times, suggests that nectar and pollen are relatively abundant. These short flights may also reduce the risk of being caught too far from the nest if the temperature suddenly drops. In cold environments, low temperatures raise the metabolic costs of flight and reduce the efficiency of foraging for pollinators (Harrison & Fewell, 2002). The strategy of using short-distance flights to take advantage of the short periods of thermally suitable weather may seem to be tenuous, but the high abundance of *E.* cf. *bicolor* in this landscape (Coates et al., 2024) indicates that it can support a thriving population. Short foraging bouts may also enable this relatively small bee to unload pollen resources more often than larger bees. This short-distance foraging pattern also means that *E.* cf. *bicolor*'s geographic presence in the landscape is closely tied to the presence of snow gum stands, which form a mosaic at the tree line and in nearby frost hollows. Their role as pollinators is also expected to diminish rapidly with distance from snow gums.

Future foraging activity under climate change

Our biophysical modelling suggests a substantial expansion in the activity window of *E.* cf. *bicolor* under future warming scenarios. While

this offers insight into how thermal constraints will relax, the scale of predicted change introduces uncertainty, particularly when considering how interacting ecological processes may influence outcomes. Biophysical models offer a framework for predicting a species' fundamental niche, but they do not account for all biotic influences that constitute its realized niche (Kearney & Porter, 2009). As such, our projections reflect physiological potential rather than direct predictions of behavioural outcomes. Other biotic factors that influence *E.* cf. *bicolor*'s survival, such as changes in competition dynamics, associations with flowers and impacts on immature life stages, will also determine their response to climate change but are not captured by our model's predictions. For instance, in *E. robusta*, warmer conditions have been linked to increased brood production and more frequent social nesting (Cronin & Schwarz, 1999a), while studies of butterflies suggest different vulnerabilities across larval and egg life stages compared to adults (Buckley & Kingsolver, 2012; Kiekebusch et al., 2024).

Given the current low bee diversity at high elevations in this area (Coates et al., 2024; Encinas-Viso et al., 2024), warming may introduce increased competition for floral resources from bees moving up from lower elevations or increased competition from less abundant bees already present in the area, such as *Lasioglossum* species (Coates et al., 2024; Encinas-Viso et al., 2022). Similar range shifts have been observed in other alpine pollinators, including *Bombus* (Pyke et al., 2016) and butterflies (Forister et al., 2010; Konvicka et al., 2003), with species moving upslope to track their preferred temperature envelope. This shift in competition dynamics may be especially pronounced at our highest sites, where *E.* cf. *bicolor* populations were most abundant but will be unable to move upslope due to the absence of wood for nesting above the current tree line. Snow gums are unlikely to keep pace with upslope shifts in climate under rapid climate change as they are slow-growing tree and are currently experiencing dieback that appears to be linked to climate change (Charerntantanakul et al., 2025). In contrast, ground-nesting bee species, which make up the majority of non-*Exoneura* bee diversity present nearby and downslope (Coates et al., 2024), are expected to be able to move more freely without losing access to required nesting sites.

Biophysical modelling indicates that *E.* cf. *bicolor*'s seasonal window will expand under climate change, which may have consequences for their association with flowers. While our models show that *E.* cf. *bicolor* will be active earlier and later in the season under warming, it is unknown how flowering times of key plants will respond to the same climate signal. Earlier flowering under climate change has been observed in some Australian alpine species (Gallagher et al., 2009), as well as in alpine systems globally (Studer et al., 2005), but responses are variable across taxa and years (Kudo, 2014) and may not match predicted shifts in early-season *E.* cf. *bicolor* foraging. Late-season foraging similarly depends on the timing and duration of flowering for different species. The predicted increase in late-season activity for *E.* cf. *bicolor* could translate into decreased foraging success, with comparable mismatches showing declining overlap between pollinators and late-flowering species in the Rocky Mountains (Iler et al., 2013) and Arctic systems (Høye et al., 2013; Schmidt et al., 2016). While such dynamics are plausible in our system, a better understanding of floral phenological responses is required to assess this risk.

Cold-climate strategies

This study indicates that the traits that make *E.* cf. *bicolor* successful in cold, high-elevation environments are distinct from those of the better-known and well-studied bees such as *Bombus*. *Bombus*, a cold-tolerant bee genus distributed on every continent except Australia and Antarctica (Williams & Osborne, 2009), display unique behavioural and physiological traits (Heinrich, 2004) that allow them to fly at temperatures as low as 5–10°C (Corbet et al., 1993). In our study, *E.* cf. *bicolor* was unable to fly below 14.5°C, with the probability of activity increasing at approximately 17°C, indicating that their physiological limits afford only a relatively narrow window for activity in this environment. Despite these indications that *E.* cf. *bicolor*'s temperature thresholds present significant limits to activity in this environment, the abundance of nests across our elevational gradient was highest at the tree line where it is coldest, with Coates et al. (2024) also demonstrating that they are abundant on flowers at these sites. *E.* cf. *bicolor*'s behaviour of nesting in well-developed branches of snow gum appears to be the key trait that allows them to persist in this environment. During the spring–summer foraging period, nesting in snow gums provides shelter overnight and during cold, inactive days, but may be even more advantageous when populations overwinter, when ambient temperatures regularly drop below −10°C at Charlotte Pass (Bureau of Meterology, 2025). In alpine environments overseas, *Bombus* queens overwinter in a state of diapause (Whitehorn et al., 2025). While the overwintering behaviour of *E.* cf. *bicolor* at our sites area is unknown, at lower elevations elsewhere in Australia, stem-nesting *E. bicolor* adults overwinter alongside developing brood (Silberbauer & Schwarz, 1995). While further research is needed, it is possible that, like lower-elevation *E. bicolor*, *E.* cf. *bicolor* females also overwinter within their nests, where the thermally buffered environment of snow gum wood may provide critical protection during sub-zero winters.

CONCLUSIONS

E. cf. *bicolor* is a previously undocumented case of a cold-adapted bee that makes up for its limited physiological cold tolerance by displaying behavioural traits that enable persistence in Australia's coldest environments. The success of *E.* cf. *bicolor* at high elevations appears to hinge on its unique wood-nesting behaviour, which likely provides it with a thermally buffered environment. In contrast to other physiologically cold-tolerant pollinators, *E.* cf. *bicolor* remains inactive during unfavourable weather, waiting for brief warm periods to forage. By sheltering in these nests and foraging for abundant nearby resources during suitable weather, *E.* cf. *bicolor* benefits from abundant floral resources and reduced competition from other bees. However, its capacity to maintain this low-effort, high-reward strategy may be

compromised under climate change. While we predict that future warming will extend the bees' foraging window, it may also introduce changes in competition dynamics, the potential for phenological mismatches and the inability to expand their range above the tree line. As warming permits more competitors to move upslope, *E.* cf. *bicolor* may face increased competition without the ability to shift its range. In this context, its reliance on nesting within snow gums may shift from an advantage to a liability. These findings highlight the vulnerability of insect pollinators to climate change, with broader implications for the stability of alpine plant-pollinator networks. Future research on *E.* cf. *bicolor*'s nesting biology (Tierney et al., in prep), ecology during other life stages, particularly while overwintering, and on their thermal ecology at other elevations (Takeshima et al., in prep) will help to reveal how they mediate survival under extreme winter conditions.

AUTHOR CONTRIBUTIONS

Joshua M. Coates: Conceptualization; methodology; data curation; investigation; validation; formal analysis; visualization; writing – review and editing; project administration; resources. **Noel Takeshima:** Writing – review and editing; writing – original draft; conceptualization. **Francisco Encinas-Viso:** Supervision; methodology; conceptualization; writing – review and editing. **Saul A. Cunningham:** Supervision; conceptualization; methodology; writing – original draft.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data used in our analyses are archived and publicly available within Dryad: https://doi.org/10.5061/dryad.x95x69pxc (Coates et al., 2026).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Sites selected for nest surveys. Each elevational band contained 3 study sites, randomly selected along Kosciuszko Road using a random number generator.

Figure S1. Examples of *E*. c.f. *bicolor* nest entrances, with the characteristic rim that individuals create at nest entrances visible. From left to right: newly excavated nest showing frass at the nest entrance, newer nest with rim not yet dried, typical older nest with rim dried to a grey colour, *E*. c.f. *bicolor* individual at the entrance of the nest.

Table S2. Relevant parameters used in *ectotherm* model.

Table S3. Candidate models included in selection process for *E*. c.f. *bicolor* foraging distance analysis.

Figure S2. Correlation between observed temperatures and predicted temperatures.

Table S4. *t*-test results from comparison of mean thermal limits (°C) for bees collected at Charlotte Pass versus Perisher study sites. *p*-values are two-sided. Welch's *t*-test was used (unequal variances).

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