RESEARCH ARTICLE

Climate change threatens the future of rain forest ringtail possums by 2050

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Abstract

Aim: The increasing frequency and intensity of extreme weather escalate the pressure of global warming on biodiversity. Globally, synergistic effects of multiple components of climate change have driven local extinctions and community collapses, raising concern about the irreversible deterioration of ecosystems. Here, we disentangle the pressure of increasing warming and frequency of extreme heatwaves on the population dynamics of tropical ringtail possums (family: Pseudocheiridae).

Location: The Australian Wet Tropics World Heritage Area.

Method: Ringtail possums' population dynamics were estimated between 1992 and 2021 using a hierarchical population model that explicitly described the state process and accounted for imperfect detection. Under our model, we propagated the estimated mechanisms governing the system by forecasting ringtails' population dynamics between 2022 and 2050. Derived from this process, we calculated the probability of absolute and quasi-extinction using different population viability thresholds.

Results: We find a strong negative effect of climate change on population dynamics, particularly extreme heatwaves, resulting in a rapid and severe decline in ringtails' population size in the last three decades.

Main Conclusions: Forecasted increases in temperature and heatwaves threaten the collapse of rain forest ringtail possums by 2050, with populations falling below viability thresholds within three decades.

KEYWORDS
Australian wet tropics, climate change, elevational shift, heatwaves, N-mixture model, population declines, Pseudocheiridae

1 | INTRODUCTION

The escalating intensity of climate change poses a strong pressure on global biodiversity (Hoegh-Guldberg et al., 2018). Species are tracking global warming by shifting their range to new suitable habitats (Chen et al., 2011), while species unable to shift are undergoing severe population declines (Freeman et al., 2018; Williams & de la Fuente, 2021) and local extinctions (Freeman et al., 2018;

Iknayan & Beissinger, 2018; Sinervo et al., 2010). However, the magnitude of species' ecological responses to climate change is not homogeneous across the latitudinal gradient, and evidence shows that tropical ecosystems are undergoing the greatest biodiversity erosion (Freeman et al., 2021).

The long-term ecological response of species to climate change is generally predictable. Indeed, observed alterations in species abundance, distributions and probability of extinction align

with expectations (Urban, 2015; Williams & de la Fuente, 2021). However, the mechanistic drivers shaping these ecological responses could be better explained by extreme weather events (Parmesan et al., 2000; Vázquez et al., 2017). The increasing number of hot days results in more intense and frequent extreme heatwaves. Heatwaves are emerging as a serious environmental threat much earlier in the tropics due to the low interannual temperature variability (Hoegh-Guldberg et al., 2018). The effects of heatwaves could have devastating impacts at the ecosystem level, resulting in substantial losses of suitable habitat and keystone species (Arias-Ortiz et al., 2018) that could induce cascading effects. For example, extreme weather conditions can affect the productivity of high-quality food items, inducing mass mortalities of populations unable to endure the extreme conditions due to the derived poor nutritional conditions (Hanya et al., 2004; Wild et al., 2019). Heat stress could also affect different aspects of reproductive function in many species, substantially reducing reproduction success and recruitment (Hansen, 2009). Moreover, temperature extremes could profoundly impact species with narrow thermal tolerance, potentially inducing direct mass mortalities and population collapses (Finlayson, 1932; Welbergen et al., 2008).

The combination of increasing mean annual temperature and frequency of extreme weather events is expected to have an escalating impact on tropical montane ecosystems (Colwell et al., 2008). In montane communities, the threat that climate change poses on species with narrow environmental tolerance (Janzen, 1967) is exacerbated by the limitation of upland species to shift to new suitable habitats (Marris, 2007). For example, physiological studies on green ringtail possums (*Pseudochirops archeri*) in the Australian Wet Tropics have highlighted their inability to cope with extreme heatwaves, with temperatures above 30°C for more than 5 h becoming biologically limiting for these upland species (Krockenberger et al., 2012). The synergistic effects of physiological and biogeographical constraints (i.e., the geographical isolation of mountaintops; Brown, 1978) of rain forest ringtail possums are expected to reduce their suitable habitat by 86% before the end of the century (Meade et al., 2018), indicative of the serious conservation concern for upland tropical ecosystems (Williams et al., 2003; Williams & de la Fuente, 2021).

Here, we analysed the long-term (1992–2021) population dynamics of endemic ringtail possums (*Hemibelideus lemuroides*, *Pseudochirops archeri*, *Pseudochirulus herbertensis* and *Pseudochirulus cinereus*) in the tropical rain forests of the Australian Wet Tropics, described as the second most important World Heritage Area and the sixth most important protected area globally (Le Saout et al., 2013). We used a Bayesian hierarchical population model that included an explicit description of the state process and accounted for imperfect detection in a mechanistic representation of the observation process. We explored the potential impact of climate change on population fluctuations by explicitly incorporating observed local temperature trends over the study period. We accounted for different dimensions of climate change by examining the additive effect of the long-term gradual warming and increased frequency of extreme heatwaves. The spatial differences in population dynamics

were accounted for by calculating site-specific exposure to thermal stress. We forecasted population size into the future to calculate the probability of absolute and quasi-extinction probability (i.e., species declining below potential thresholds of viable population size) of ringtail possums by 2050. We predicted that climate change would strongly influence ringtail population dynamics due to their known physiological limitations to high temperatures (Krockenberger et al., 2012). However, we expected interspecific differences among ringtail species in response to different components of climate change due to potential differences in thermal tolerance and ecology not conserved across taxa. Finally, we expected interspecific differences in the overall population trajectory due to differences in the elevational range these species occupy. Species restricted to the highlands are expected to undergo greater population declines than species occurring at lower elevations due to the impossibility of upland species shifting their range as they track climatic changes (i.e., "the escalator to extinction"; Marris, 2007; Urban, 2018).

2 | METHODS

2.1 | Study area

The Australian Wet Tropics bioregion is composed of approximately 7000 km² of mixed tropical rain forest (de la Fuente et al., 2022). The region is dominated by mountain ranges, where elevation is the predominant gradient shaping the biodiversity and ecological processes (Williams et al., 1995). The elevational gradient spans from the sea level to highlands at 1000 m, with isolated peaks reaching up to 1620 m (Figure S1; Nix & Switzer, 1991). Despite the loss of rain forest that followed European Settlement (Woinarski, 2010), large areas of continuous rain forest persist in the region within the Australian Wet Tropics World Heritage Area (Figure S2).

2.2 | Study species

The ringtail possum community inhabiting the rain forest of the Australian Wet Tropics is composed of four species: *Hemibelideus lemuroides*, *Pseudochirops archeri*, *Pseudochirulus herbertensis* and *Pseudochirulus cinereus*. This community represents an iconic component of the Outstanding Universal Value of the Wet Tropics World Heritage Area (Williams et al., 2010). Ringtails are nocturnal, arboreal marsupials that feed predominantly on foliage (Goudberg, 1990; Jones et al., 2006). They have similar morphology with average mass and body length ranging from 945 to 1185 g and from 268 to 753 mm (Winter et al., 2004). Their life span ranges from 4 to 6 years in the wild, with an estimated average generation time of 4 years (Springer & Kirsch, 1989). The elevational and environmental range of these species overlaps greatly (Figure S3), except for *Pseudochirops archeri*, which has the lowest historical lower elevational limit (300 m a.s.l.; historical core population centred between 600 and 700 m; Williams et al., 2010; Winter et al., 2004). The core population of *Hemibelideus*

lemuroides and *Pseudochirulus herbertensis* is found between 800 and 1000 m in elevation, with a historical elevational range spanning from 450 to >1200 m (Williams et al., 2010; Winter et al., 2004). *Pseudochirulus cinereus* and *Pseudochirulus herbertensis* are latitudinally segregated and do not overlap, with *Pseudochirulus cinereus* restricted to the highlands of northern mountain ranges above 800 m in elevation (Figure S4).

2.3 | Ringtail possum surveys

The long-term possum monitoring scheme was established in 1992 to study population trajectory of ringtails under the pressure of climate change. Since then, 1069 surveys have been conducted across the elevational gradient of the mountain ranges within the region. Of the 32 independent sites monitored, we selected for this study those sites with at least one observation in more than 1 year ($n = 19$), discarding sites that were outside the distribution of the study species. All study sites were selected to be within large patches of rain forest, avoiding habitat edges. Sites in the northern part of the Wet Tropics were not established until 2004, which explains the shorter time series analysed for *Pseudochirulus cinereus*. The combination of these sites covers approximately 94% of the available climatic space within the rain forests of the region (Williams et al., 2010). Study sites were defined by a 1000 m transect on a small road/track that provided reasonable visual access to the full forest structure up to the rain forest canopy. Survey effort and methodology were maintained constant since 1992. Spotlight surveys were conducted by 2–3 observers walking at a standardized pace of 4–5 min of searching per 100 m with a total search time of between 40 and 50 min.

2.4 | Climate change covariates

Temporal climate information was obtained from Walkamin Research Station (594 m a.s.l.; Bureau of Meteorology, 2021), located in the core of ringtails' distribution (Figure S3). We obtained observed mean annual temperature and number of days with temperatures over 35°C (97.5th percentile of maximum temperature) between 1985 and 2021, allowing the examination of the impacts of climate influence in multiple dimensions: gradual global warming and increase of extreme heatwaves. Gradual warming was included to account for the long-term impact on population dynamics (Urban, 2018), while the extreme heatwaves predictor accounted for rapid fluctuation in population related to ringtails' physiological limitations (Krockenberger et al., 2012). We calculated the moving average for these parameters using an 8-year window (Figure S4). This allowed accounting for potential delays in population responses to a changing environment. Using the local climatic trends from Walkamin Research Station (Bureau of Meteorology, 2021), we calculated the expected climate fluctuation (mean annual temperature and number of hot days) between 2022 and 2050 for population predictions using generalized additive models (*climatic variable ~ time*; Figure S5;

Wood, 2011). The model accurately captured the temporal variation in the climatic trend (deviance explained = 81.7% for mean annual temperature and 97.3% for number of hot days), indicating a robust fit for climatic forecasting (Figure S5).

The linearity of the expected increase in temperatures matched the predicted warming trend between 2021 and 2050 obtained using global climate models (Arias et al., 2021; Suppiah et al., 2007). However, forecasting stochastic events, such as heatwaves, can be challenging. Our prediction of heatwaves was based on the assumption that, in the tropics, the frequency of heatwaves is expected to increase with global warming due to the low interannual temperature variability (Hoegh-Guldberg et al., 2018). Thus, following the expected linear increase in temperature between 2022 and 2050 and the observed linear increase in heatwaves in the last decade (2012–2021; Figure S4), we assumed a consistent increasing pattern in heatwave events between 2022 and 2050.

The spatial component of climate change was calculated as an index of climatic exposure at each study site (de la Fuente et al., 2021). This index was estimated as the area under the curve using interpolated monthly maximum temperature averages between 1970 and 2018 (Harris et al., 2014). The threshold to define the area under the curve was obtained from the 97.5th percentile of maximum temperature within the climate envelope of ringtail possums (Williams et al., 2010). Thus, the index represents the combination of both the intensity and duration of unfavourable thermal conditions for ringtail possums at a specific site relative to the species' environmental range (i.e., the conditions experienced by the species at any given point throughout their distribution), with a high index meaning intense and prolonged exposure to high temperatures. In contrast, a low index indicates sites close to the lowest exposure of the species across its distribution. Thus, the climatic exposure index provides a biologically relevant predictor for spatial differences in population size, as it accounts for the species' environmental limits and the elevational, latitudinal and topographic gradients influencing temperature.

2.5 | Population model

We adopted an dynamic binomial mixture model to analyse the temporal variation in ringtail possum populations (Kéry et al., 2009). These models estimate species abundance from count data while accounting for imperfect detection (Royle, 2004). Detection probability is estimated using spatiotemporal replicated count surveys. This information is then used to approximate the true abundance from the variation in observed local abundance. Thus, binomial mixture models are hierarchical models composed of two linked processes: state or ecological process and observation process (Royle, 2004).

The ecological process assumes that the unobserved true local population size at site *i* in year *t* (N_{it}) is described by a Poisson distribution with latent abundance λ_{it}. We accounted for the additive effect of climate change on the spatiotemporal variation in abundance by including observed and estimated climatic covariates that

could influence the temporal and spatial fluctuation in ringtail possum populations:

$$N_{(it)} \sim \text{Poisson}\left(\lambda_{(it)}\right)$$

$$\log\left(\lambda_{(it)}\right) = \alpha_{\text{region}} + \beta_w w_{(t)} + \beta_e e_{(t)} + \beta_{ts} ts_{(i)} + \beta_g (t - \text{midpoint})$$

where α_{region} defines the intercept of the model (the log rate in year 1992), β_w accounts for the effect of temporal variation in gradual regional warming (w_t), β_e accounts for the effect of temporal fluctuation in extreme temperatures (e_t), β_{ts} accounts for the effect of spatial variation in climate exposure (ts_i), and β_g accounts for the extra variation in population trajectory not explained by climate change. This temporal trend estimate was defined by subtracting the midpoint from each integer year ($t - \text{midpoint}$). Indexes define the dimension of variation for each covariate as either spatial (i) or temporal (t). We expected a priori potential differences in population trajectory in different sites, so we also explored the possibility of fitting a random-slope model to allow slope variation among sites. However, the model with site as random effect did not achieve convergence, likely due to the low number of independent sites with a robust temporal representation of population fluctuation along the time series. Thus, the model developed here focussed on calculating regional summaries of the temporal fluctuation of ringtail possum populations rather than site-specific trajectories. Potential differences among sites were accounted for by the spatial climatic exposure variable, which is 96% correlated with elevation. This allowed estimating the influence of the temporal climatic variables after accounting for potential climate-induced elevational shifts.

In addition to estimating the additive linear effect of the climatic variables on population dynamics, we explored the potential for significant thresholds of population responses to environmental conditions. The changepoint analysis was performed by adding a piecewise regression component to the temporal climatic variables of the model (i.e., global warming and extreme heatwaves). To decide whether significant changepoints in the climatic variables influenced population dynamics, we evaluated the strength of slope changes at all the potential changepoints. However, due to the low level of confidence surrounding inflection points in climatic effects (Figure S6), the state process in the final population dynamic model did not include the changepoint component, achieving a more parsimonious model while respecting the rules of marginality (McCullagh & Nelder, 2019).

The observation process is the mechanistic representation of the detection process. The observation process assumes that detection probability p is represented by the observed counts (y_{it}) from the local population (N_{it}) in each replicate j (C_{ijt}), which is described by a binomial distribution:

$$C_{(ijt)} \mid N_{(it)} \sim \text{Binomial}\left(N_{(it)}, p_{(ijt)}\right)$$

$$\text{logit}\left(p_{(ijt)}\right) = \alpha_{year(t)} + \beta_{date}\text{date}_{(ijt)} + \varepsilon_{(ijt)}$$

where α_{year} defines the intercept for detection fitted for each year, while β_{date} accounts for the effect of the Julian date on detectability

(date$_{ijt}$; Figure S9). Additionally, we accounted for extra unexplained heterogeneity among surveys in detection probability not captured by covariates by fitting a normally distributed random effect (ε_{ijt}).

We computed the absolute and quasi-extinction probabilities for each ringtail possum species by forecasting population size into the future. We used the predicted gradual increase in mean annual temperature and increase in extreme heatwave events (Figure S5) to capture the variation in the forecasted population size estimations given the model (Schaub & Kery, 2021). Quasi-extinction probability thresholds (i.e. minimum viable population size) were derived from the IUCN criteria used to evaluate threatened categories (IUCN, 2012). We derived the probability of each species reaching a population loss threshold of 50%, 70%, 80%, 90% (quasi-extinction) and 100% (absolute extinction) between 2022 and 2050 across the study sites. The initial population size used to calculate the minimum viable population threshold was selected *post-hoc*, using the estimated mean minimum population size prior to an observed population recovery (1997 for *Hemibelideus lemuroides*; 1992 for *Pseudochirops archeri*; 1992 for *Pseudochirulus herbertensis*; and 2004 for *Pseudochirulus cinereus*). Thus, these quasi-extinction thresholds provided a realistic approximation of critical minimum viable population size for ringtail possums utilized in national and international assessments of extinction risk.

We fitted the dynamic binomial mixture model using Bayesian inference. Markov Chain Monte Carlo (MCMC) methods were used to sample the joint posterior distribution (Thompson & Brooks, 2003) using JAGS (Plummer, 2003), called from R (R Core Team, 2021), with the *jagsUI* package (Kellner, 2021). We ran three parallel chains of 500,000 iteration each, used the first half as burn-in and thinned the rest by one in 100 to obtain 7500 samples of the joint posterior distribution. The sampling process led to acceptable convergence of all parameters ($\hat{R} - 1 < 0.1$, (Gelman & Hill, 2006)). We examined the adequacy of the model by computing a Bayesian p-value (Kéry et al., 2009). Values ranging from 0.5 to 0.53 indicated a good fit for all species modelled. We expressed the absence of prior information about the model parameter by implementing vague priors obtained from Kéry et al. (2009). We selected uniform distributions (-5, 5) for α_{region}, β_w, β_e, β_{ts} and β_{date}, uniform distribution (-1, 1) for β_g, uniform distributions (0, 1) for α_{year}, uniform distribution (0, 10) for the standard deviation of the overdispersion factor for detection and uniform distribution (-2, 2) for the changepoint.

3 | RESULTS

3.1 | Overall changes in population size

The population dynamics of ringtail possums in the Australian Wet Tropics showed pronounced negative responses to climate change. All species underwent marked population changes over the last 30 years, resulting in rapid population declines since 2010. Furthermore, the predicted increase in mean annual temperature and frequency of heatwaves is expected to induce further severe population losses, threatening the collapse of the ringtail possum assemblage by 2050 (Figure 1). As expected, species restricted to higher

elevations (i.e., *Hemibelideus lemuroides* and *Pseudochirulus herbertensis*) showed greater declines in population than species with a wider elevational range (i.e., *Pseudochirops archeri*). *Hemibelideus lemuroides* fluctuated in population size between 1992 and 2011, followed by a severe decline that resulted in a mean net population loss of 68.2% in only 11 years (Figure 1). *Pseudochirulus herbertensis* underwent a consistent population decline since 1997, showing a mean net population loss of 65.5% compared with the initial population size in 1992 (Figure 1). *Pseudochirops archeri* showed a strong population increase between 1992 and 2014, indicating an early population expansion into the uplands, with the first record of the species at the sites above 1100 m in elevation in 2009. However, the population trajectory reversed in 2014, with a consistent population decline thereafter (Figure 1). *Pseudochirulus cinereus*, despite presenting an overall positive population growth (Figure 2), underwent a mean net population loss of 57.3% relative to 2004. However, the population estimates of *Pseudochirulus cinereus* showed great uncertainty (Figure 1), likely due to the small distributional range of the species, with population dynamics derived from only four sites (Figure S3).

3.2 | The effect of temporal changes in the regional temperature

The temporal variation in ringtail populations was strongly correlated with regional changes in temperature (Figure 2; Figure S7 and S8).

The increasing frequency of heatwaves had a strong negative effect on the population size of *Hemibelideus lemuroides* and *Pseudochirops archeri* and a weak negative influence on *Pseudochirulus cinereus* (Figure 2). In contrast, the increase in mean annual temperature had a strong negative correlation with *Pseudochirulus herbertensis* and *Pseudochirulus cinereus*' population dynamics and a weaker negative effect on the population size of *Pseudochirops archeri* (Figure 2). Interestingly, a proportion of the variation in the population dynamics was positively correlated with mean annual temperature for *Hemibelideus lemuroides* and to extreme heatwaves for *Pseudochirulus herbertensis* (Figure 2). *Hemibelideus lemuroides* showed a positive correlation with gradual warming in the first half of the time series, but this trend was reversed with an overall increase in temperature of >0.27°C compared with 1997 (i.e., lowest annual mean temperature; Figure S7). Similarly, *Pseudochirulus herbertensis* showed positive synchronization with the early fluctuation in the number of heatwaves, but the changepoint occurred with a >1.76 increase in the number of hot days compared with 2002 (Figures S6 and S7). The effect of the additional temporal variability in population trajectory not captured by climatic variables was overall weaker for all species (Figure 2; Table S1), suggesting that climate change was the predominant driver of ringtails' population dynamics.

The changepoint analysis attempted to identify thresholds of significant change on the influence of the climatic variables on ringtail possum population dynamics. The changepoints associated with global warming and extreme heatwaves showed a clear
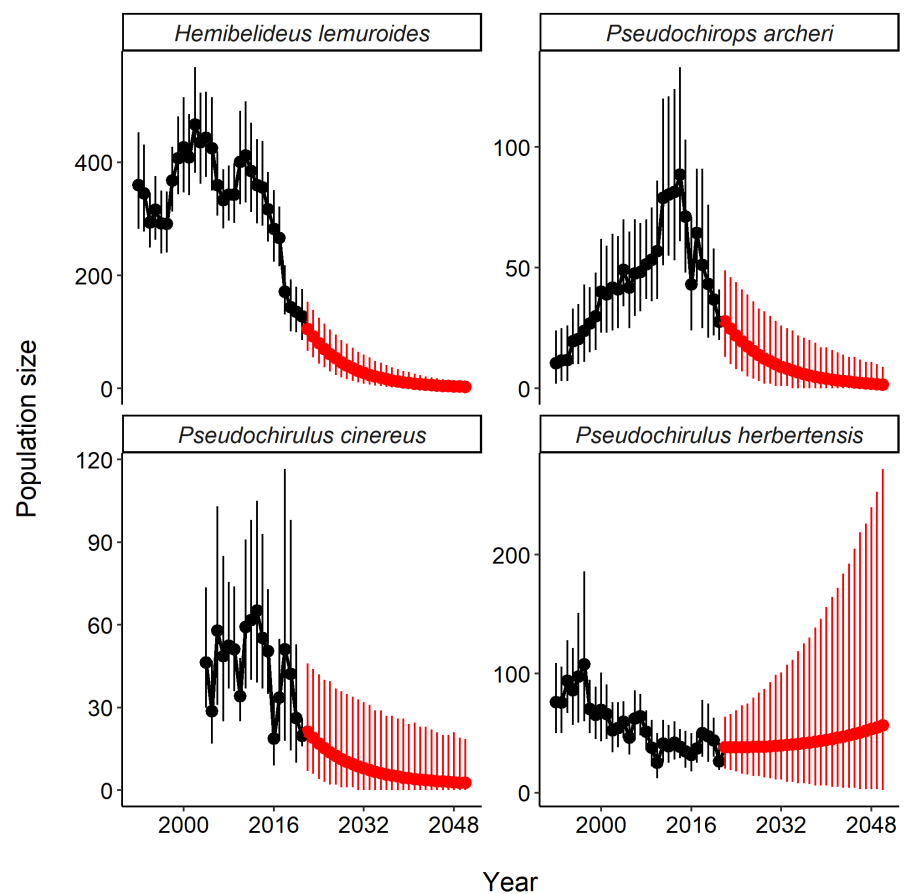

FIGURE 1 Temporal changes in ringtail possum population size between 1992 and 2050. Points represent the posterior mean and the 95% CRI derived from our dynamic mixture model. Black values represent the estimations derived from the observed data (1992–2021), while red values depict the predicted population size given the forecasted pace of climate change (2022–2050; Figure S5).
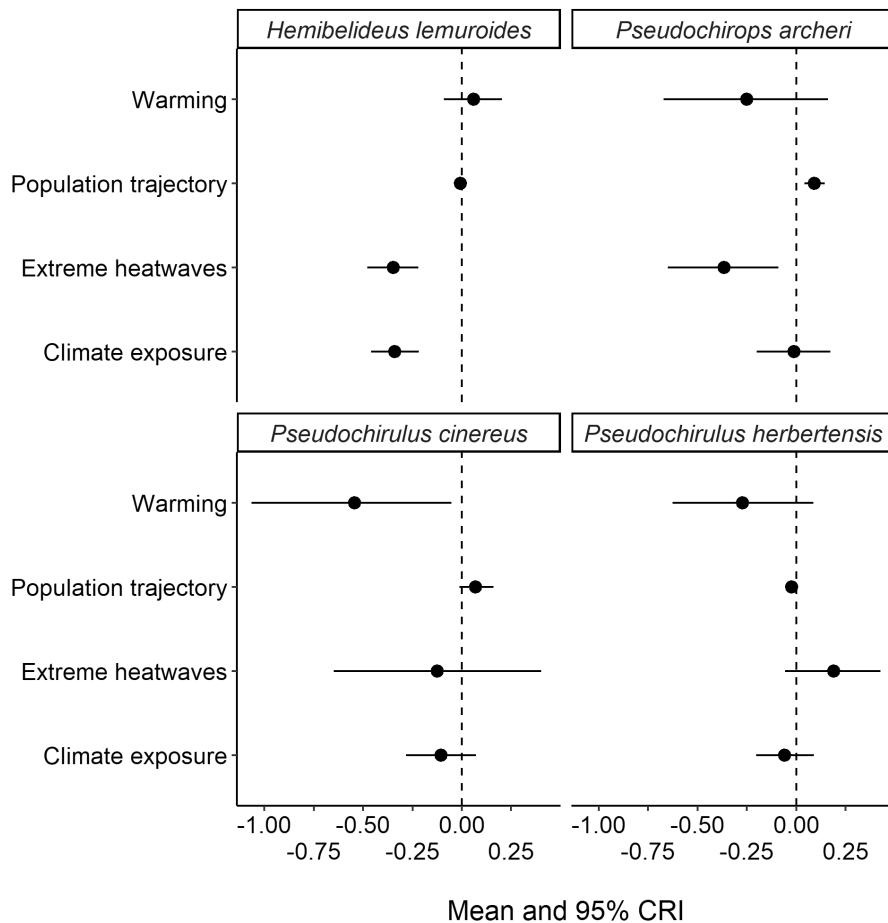
FIGURE 2 Estimated influence of each environmental variable on the observed population dynamics of each ringtail possum species. Parameter estimates based on summaries of the marginal posterior distribution. We reported the mean and 95% credible interval (CRI). The coefficients monitored represent the effect of the trend in mean annual temperature (β_w), the effect of extreme heatwaves (β_e), the overall population trajectory after accounting for temporal climatic variables (β_g) and the effect of site-specific climatic exposure (β_{ts}). A table with all model parameters can be found in Table S1. A visual representation of the relationship between the estimated population size and climatic variables can be found in Figure S8. The temporal fluctuation in detectability derived from the observation process can be found in Figure S9.

pattern of temporal similarity among species (Figure S6). Potential changepoints induced by global warming ranged between 0.21 and 0.38°C increase, likely occurring between 2010 and 2016 (Figure S4). Similarly, changepoints in population dynamics influenced by extreme heatwaves were closely associated with the period of linear increase in the frequency of heatwaves between 2011 and 2021 (Figure S4), with potential changes in slope induced by an increase in the number of hot days between 1.76 and 3.63. Despite the observed pattern in the relative influence of climatic variables (Figure S7), the uncertainty associated with these changepoints was high (Figure S6). The high uncertainty in changepoint patterns was likely related to the strong linear effect of the climatic variable inducing negative population growth and the inherent uncertainty associated with the climatic variable inducing the early population increase (Figure 2).

## 3.3 | The effect of spatial climatic exposure on abundance

The spatial variation in thermal exposure negatively influenced population size for all species, suggesting reduced ringtail populations in sites with higher exposure to extreme temperatures (i.e., at lower elevations; Figure S8). However, the strength of the relationship was more evident for high-elevation species (*Hemibelideus lemuroides*,

Pseudochirulus cinereus and *Pseudochirulus herbertensis*; Figure 2; Table S1, Figure S8). The low influence of the climatic exposure index on *Pseudochirops archeri* was expected, given the wider environmental range occupied by this species (Figure S3).

3.4 | Extinction probability of ringtail possums between 2022 and 2050

Our model predicted a very high probability of continuous decline for *Hemibelideus lemuroides*, *Pseudochirops archeri* and *Pseudochirulus cinereus* between 2022 and 2050. *Hemibelideus lemuroides* have already reached an average net population loss of >50% relative to 1997 (i.e., minimum population size prior to an observed recovery; Figure 1), with a high probability (>75%) of reaching 70%, 80% and 90% net population loss in the next 4, 8 and 13 years, respectively (Figure 3). This level of decline based on observed population changes currently places *Hemibelideus lemuroides* into the IUCN *Endangered* category (Criteria A2), with a high probability of them becoming *Critically Endangered* within a decade. Similarly, *Pseudochirulus cinereus* is predicted to undergo a severe net population loss, reaching a 90% decline within the next two decades. The projected response of *Pseudochirops archeri* showed delays in quasi-extinction probabilities compared with other ringtail possums due to the initial increase in population size between 1992 and 2014 (Figure 1), where

FIGURE 3 Absolute (100% population loss) and quasi-extinction probabilities (population viability threshold) of ringtail possum in the Australian wet tropics between 2022 and 2050. Extinction thresholds were derived from the IUCN threatened categories (IUCN, 2012).
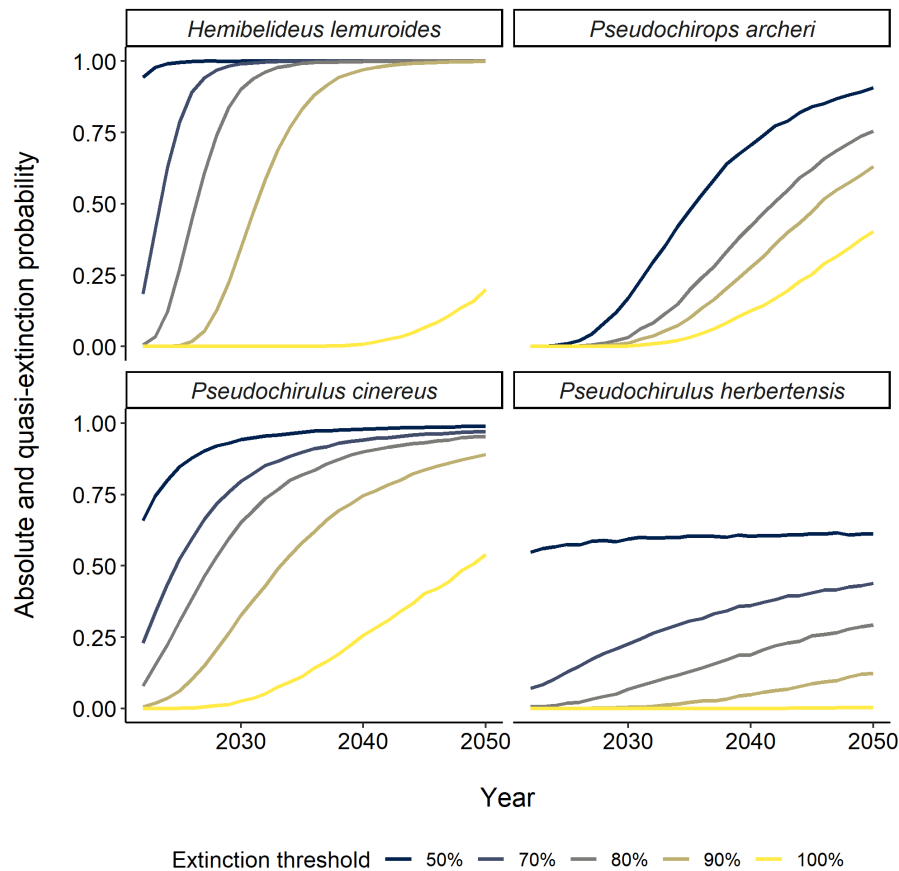
the population had expanded and increased into higher elevations. Our model showed a high probability (>75%) of 50% reduction in *Pseudochirops archeri* population (relative to 1992) and a moderate probability (>50%) of 70%–80% net population loss by 2042 (Figure 3). Finally, despite the robust estimates of the observed population dynamics for *Pseudochirulus herbertensis*, the additive effect of climatic variables did not capture the variability in the forecasted population size (Figure 1). Thus, the predicted extinction probabilities held a great uncertainty for this species (Figure 3). Nevertheless, based on observed population declines, *Pseudochirulus herbertensis* should be considered as *Vulnerable* under IUCN Criteria A2 (currently listed as *Least Concern*; Burnett & Winter, 2016).

4 | DISCUSSION

Several decades of research on species response to climate change have evidenced the threat that global warming poses to communities and ecosystems worldwide (Arias et al., 2021). Indeed, local extinctions and community collapses have been attributed to the direct effect of climatic changes (Freeman et al., 2018; Hanya et al., 2004; Iknayan & Beissinger, 2018; Pounds et al., 1999; Sinervo et al., 2010). However, the drivers of species responses to climate change are not always evident. Our results showed the severe impact of regional warming and the increased frequency of heatwaves on ringtail possums dynamics, resulting in marked declines in population over the last 30 years. Moreover, these population losses are expected to

escalate in the following decades, threatening the survival of rain forest ringtail possums by 2050.

4.1 | Overall population trajectories

The overall trajectory among ringtail possums matched a priori expectations of montane species responses to global warming (Marris, 2007; Urban, 2018). Species restricted to high elevations showed severe population declines, with an average net population loss above 60% in 30 years. Contrastingly, species with a wider elevational range (i.e., *Pseudochirops archeri*) showed a consistent early increase in population, resulting from a population expansion into higher, cooler parts of their distribution. However, regional increase in temperature and frequency of extreme heatwaves since 2010 induced a changepoint in the trajectory of the latter population, with a linear decline thereafter. This pattern in population trajectory is not unique to ringtail possums in the region. Rain forest birds have followed a similar trend, with midland specialist species showing a steady population increase between 2000 and 2008 followed by a continuous decline, while upland bird species showed consistent population losses across the entire region throughout the examined period (Williams & de la Fuente, 2021). This pattern could reveal important tolerance thresholds for species with the potential to shift to new suitable habitats as they track climatic changes. Nevertheless, as our results indicated, even species adapted to a wider environmental

range might not have sufficient plasticity to cope with the rapid pace of climate change (Arietta & Skelly, 2021).

4.2 | Spatial sensitivity to climate change

The inclusion of a spatial climatic dimension in the model allowed examining the effect of spatial variability in climatic exposure across the species distributions. Our results indicated that population dynamics were negatively influenced by exposure to intense and prolonged extreme heatwaves (Figure S8). Population size showed a negative correlation with increasing exposure for upland-restricted species (i.e., *Hemibelideus lemuroides*, *Pseudochirulus cinereus* and *Pseudochirulus herbertensis*), suggesting that higher elevations species could be undergoing greater population losses at their lower elevational limit. However, the effect of climate exposure on ringtail populations was not observed on species with a wider environmental niche (i.e., *Pseudochirops archeri*). The effect of the elevational gradient on ringtails' responses to climate change aligns with the observed rapid elevational contraction of tropical montane biodiversity (Freeman et al., 2021), highlighting the escalating biotic perturbation and extinction risk of montane ecosystems under the pressure of climate change (La Sorte & Jetz, 2010).

4.3 | Temporal effect of global warming

The fluctuation in population changes in ringtail possums between 1992 and 2021 was largely explained by different dimensions of climate change. Our results suggested that potential evolutionary tolerance to a rapidly changing environment might not be preserved across ringtail possum species. Interestingly, species within the same family showed different responses to different climatic dimensions, despite the great overlap in their environmental niche (Figure S3). As Meade et al. (2018) predicted using physiological models based on Krockenberger et al. (2012), *Pseudochirops archeri* showed the greatest response to an increase in the frequency of extreme heatwaves compared with other ringtail possums. The negative effect of heatwaves was also severe for *Hemibelideus lemuroides*, with population dynamics tracking the fluctuation in the number of hot days (Figure S8). Contrastingly, members of the genus *Pseudochirulus* (*Pseudochirulus herbertensis* and *Pseudochirulus cinereus*) showed a greater negative population synchronization with a gradual increase in mean temperature. The marked differences in response to climate change among ringtail species could have profound implications for conservation. While gradual warming can be accurately predicted and the potential impacts are also likely to be gradual, the stochasticity related to the rapid increase in heatwaves (Hoegh-Guldberg et al., 2018) could have fast and devastating impacts on these vulnerable populations (Krockenberger et al., 2012; Parmesan et al., 2000).

4.4 | The fate of ringtail possums

Our results showed that the escalating pace of climate change in the Australian Wet Tropics is likely to increase the pressure on rain forest ringtail possums in the following decades, threatening the species' survival. The minimum viable population analysis showed a high probability of species reaching critical declining thresholds, with populations undergoing losses of up to 90% by 2050. These projections are subject to the consistency of the observed climatic trends, although limiting warming in the following decades might now be beyond reach (Hoegh-Guldberg et al., 2018). The observed trajectory of ringtail possum populations means the realization of the predictions about climate change impacts on montane ecosystems (McDonald & Brown, 1992), with an early extirpation of marginal populations likely escalating to the extinction of entire upland tropical species (de la Fuente et al., 2022; Urban, 2018). However, as indicated by the effect of climatic exposure on populations across the elevational gradient, we could expect delays in population responses at elevations above 1200 m, where the current exposure to extreme heatwaves is low compared with lower elevations. Nevertheless, despite the potential slower degradation of populations in the mountaintops, rain forest habitat extending above 1200 m represents small areas (<2%; 136 km², de la Fuente et al., 2022) with high isolation (i.e., "mountain islands"; Brown, 1978). Thus, the idea of remnant high-altitude rain forest areas as the sole long-term stronghold for ringtail possum populations might be limited.

This study supports the hypothesis that climate change is inducing a rapid contraction of ringtails' suitable habitat due to the increasing physiological pressure associated with thermal stress (Krockenberger et al., 2012; Meade et al., 2018). The severe declines that ringtail possums are undergoing might be exacerbated by climate-induced changes in the nutritional and toxicological landscape (Beale et al., 2018; Rothman et al., 2015). In this regard, the feeding rate of marsupial folivores could substantially decrease with hotter temperatures, explaining the escalating reduction in ringtails fitness with climate change (Youngentob et al., 2021). In this context, the effect of climate change on nutritional stress should be considered as a potential synergistic effect increasing the direct physiological pressure induced by thermal stress (Beale et al., 2022). This hypothesis would align with the description of the ecological correlates of ringtail possums abundance in the Australian Wet Tropics (Kanowski et al., 2001), where a relationship between foliage nutritional quality and ringtail possum abundance was suggested.

5 | CONCLUSION

This study has demonstrated that the imminent collapse of the rain forest ringtail possums is directly associated with climate change. We suggest that the profound biodiversity deterioration observed over the last decades in the Australian Wet Tropics (Williams & de la Fuente, 2021) might be a widespread pattern in montane

ecosystems worldwide (La Sorte & Jetz, 2010), threatening a significant proportion of the global biodiversity (Manes et al., 2021). Separating the relative impacts of increasing means and extremes temperatures and identifying climatic thresholds for tipping points in population declines provides significant insights into the potential adaptation actions to minimize future impacts. Management actions associated with extreme events are potentially very different from those aimed at increasing resilience to gradual climatic changes. The relatively short temporal scale of extreme events may enable rapid and targeted management interventions not possible for impacts associated with longer-term changes in mean conditions.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data and code to reproduce all analyses are available at doi: https://doi.org/10.5061/dryad.m63xsj44h.

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BIOSKETCH

Alejandro de la Fuente is a PhD candidate at James Cook University. He is mainly interested in investigating how montane rain forests species respond to climate change in order to translate novel ecological knowledge into practical conservation actions and management plans.

SUPPORTING INFORMATION

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

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