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Climate-Induced Physiological Stress Drives Rainforest Mammal Population Declines

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ABSTRACT

Climate change is a major driver of global biodiversity loss, yet the precise mechanisms linking climate change to population declines remain poorly understood. We developed a novel, broadly applicable framework that integrates biophysical, nutritional, and population modeling to capture fundamental physiological constraints on mammalian herbivores and applied it to investigate the causes of declines in ringtail possums of the Australian Wet Tropics (*Pseudocheirus archeri* and *Hemibelideus lemuroides*). Our approach bridges the gap between mechanistic (“bottom-up”) models, which simulate species’ responses based solely on their traits and local microclimates, and the more common (“top-down”) statistical models, which infer species’ responses from occurrence or abundance data and standard environmental variables. We quantified population dynamics over a 30-year period by generating species-specific estimates of temperature and water stress, foraging limitations, and linking these with annual monitoring and nutritional quality within an open population model. Our findings demonstrate that climate change has impacted populations through physiological stress, but in a species-specific manner. Both species have experienced population collapses at lower elevations and in low-nutritional sites. For *P. archeri*, we found evidence that population changes were driven by reduced survival due to overheating and dehydration, alongside diminished recruitment from limited foraging. In contrast, our model suggests that *H. lemuroides* populations were primarily affected by foraging constraints, emphasizing the importance of considering climate-driven limitations on foraging activity in addition to direct physiological stress. These mechanistic insights offer a foundation for targeted conservation strategies to mitigate the impacts of climate pressures on wild populations.

†Andrew K. Krockenberger passed away in March 2025. He contributed significantly to all stages of this research, and his long-term work underpins the foundations of this paper. This manuscript stands as a tribute his lasting intellectual and scientific contributions as our valued mentor, colleague, and friend.

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1 | Introduction

Anthropogenic climate change is exposing ecosystems to increasingly extreme conditions, negatively impacting global biodiversity (Hoegh-Guldberg et al. 2018). While the link between climate change and species decline is well documented, the underlying mechanisms that determine how species respond to changing conditions remain poorly understood (Briscoe et al. 2023; Buckley et al. 2023; Helmuth et al. 2005). Failing to capture the complexity of species responses to climate change often leads to a mismatch between model predictions and observed responses (Urban et al. 2016). This lack of mechanistic insight hampers advances in conservation and global change biology because, without knowledge of the underlying processes, we have limited management levers and reduced capacity to anticipate threats (Briscoe et al. 2023; Buckley et al. 2023).

To capture the complexity of climate change impacts on species, it is critical to link individual-level physiological performance outcomes with broader population dynamics. Mechanistic models, based on biophysical ecology, address this challenge by applying the principles of physics and chemistry to capture species' thermodynamic constraints linked to mass and energy exchange (Kearney et al. 2021; Kearney and Porter 2017, 2020). By quantifying the heat, water, and chemical energy balances of organisms in natural environments,

the output of biophysical models can translate to metrics of physiological and ecological performance (Gates 1980; Porter et al. 1973, 2000), providing insight into how environmental stress affects vital rates and life history (Kearney 2012). Integrating biophysical processes into population models is the next crucial step needed to predict how climate-induced stress at the individual level scales up to influence population dynamics, but very few studies have bridged this gap (Briscoe et al. 2023; Buckley 2008; Kearney 2012; Kearney, Briscoe, et al. 2010; Riddell et al. 2019).

We develop a novel modeling approach to unravel the mechanisms driving climate-induced population declines by integrating nutritional and eco-physiological constraints into population dynamics. The framework comprises three modules (Figure 1): a biophysical model quantifying the links between functional traits, microclimates, and physiological stress; a resource model defining the nutritional landscape; and a population dynamic model linking physiological limitations and resource availability to population outcomes. This biophysically informed population model connects observed changes in abundance to predicted alterations in physiological stress and constraints in resource availability, allowing inferences of the mechanisms driving climate-induced ecological responses.

To illustrate this approach, we applied it to a high-priority conservation region, the Australian Wet Tropics, which is experiencing severe biodiversity loss associated with rapid

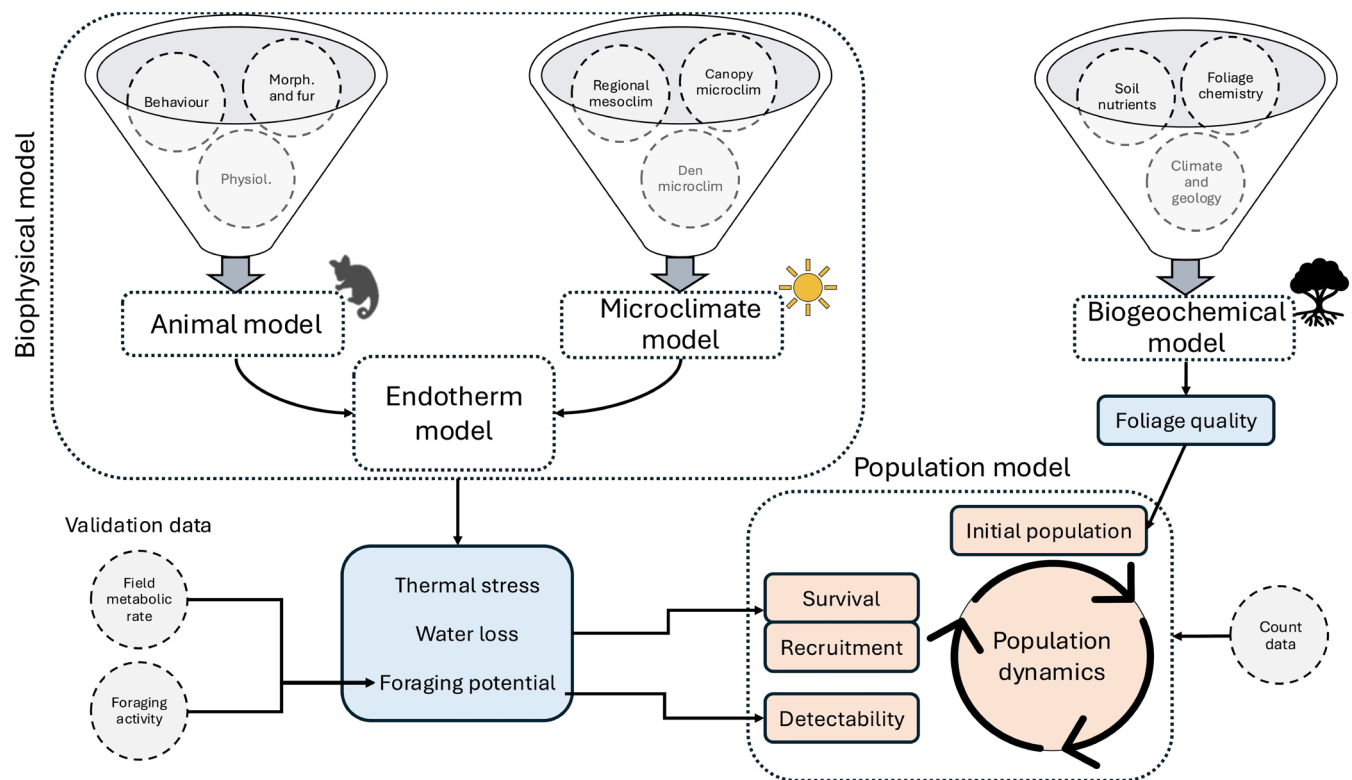


FIGURE 1 | Conceptual illustration of the integrated modeling approach. Gray circles denote datasets used to parameterize and validate the models. Dotted white rectangles outline the principal models within the framework, while blue rectangles represent derived parameters that integrate the biophysical and biogeochemical processes into the population model. Note that hourly weather data, soil, and topographic information are also inputs to the microclimate model but are derived from generic, open data sources and omitted in the figure. Additionally, some variables considered in the population model (e.g., elevation, density dependence effects, number of surveyors) are not derived from the outlined processes and therefore omitted here.

climate change (de la Fuente et al. 2023; de la Fuente and Williams 2022; Williams and de la Fuente 2021). Over three decades of monitoring have revealed strong correlations between rising temperatures and population declines in endemic rainforest ringtail possums (family Pseudocheiridae), pushing these phylogenetically distinct species to the brink of extinction, with some projections suggesting their functional extinction of these species by 2050 (de la Fuente and Williams 2022).

While previous research has established strong correlations between rising temperatures and population declines (57%–68% from 1992 to 2021), the mechanistic pathways driving these declines remain unclear (de la Fuente and Williams 2022). Specifically, it is not well understood how climate change alters key physiological, ecological, and demographic processes to ultimately reduce population viability in natural ecosystems. Without explicitly linking behaviour, physiological stress, resource availability, and demographic responses, it remains challenging to assess why these species are declining and, more critically, which factors are the primary drivers of population collapse. This system provides a rare opportunity to critically test this biophysically informed population model, leveraging decades of ecological and physiological research documenting the rapid collapse of ringtail populations.

One of the most notable climate-driven stressors in this system is the increasing frequency and intensity of heatwaves (de la Fuente and Williams 2022). Weather data from the Walkamin Research Station (594 m a.s.l.), located near the centre of the ringtails' range, indicates that the number of extreme hot days (above 35°C) has doubled from 1992 to 2022 (Bureau of Meteorology 2023). The trend in extreme heat events has followed a curvilinear trajectory, with a period of relative stability between 1997 and 2012, followed by an exponential increase in extreme heat days from 2012 to 2022, surpassing historical records since 2016 (de la Fuente and Williams 2022). These extreme events likely exacerbate thermal stress and metabolic constraints, particularly for high-elevation specialists that are poorly adapted to sustained heat exposure (Krockenberger et al. 2012).

Experimental studies suggest that marsupial folivores like ringtail possums face severe challenges in coping with extreme heat, with overheating and dehydration likely limiting their survival and recruitment (Krockenberger et al. 2012; Turner 2020). Climate-induced physiological stress can disrupt their feeding ecology, significantly reducing food intake which, in turn, diminishes breeding success (Beale et al. 2022, 2023; Kearney, Wintle, et al. 2010; Parker et al. 2009). The decline in foraging performance associated with increased temperatures could be exacerbated in these species due to low energy reserves, critical for enduring extreme conditions (Rübsamen et al. 1984; Youngentob et al. 2021). Collectively, the empirical evidence suggests that physiological stress from a warming climate could threaten the viability of ringtail possum populations. However, the conditions in experimental studies often fail to capture the complex, multidimensional factors that animals must balance in nature, reducing certainty about how the findings might translate to wild populations.

To test these ideas in a more holistic manner, we used the biophysical model to generate metrics of chronic and acute heat and water stress through space and time in ringtail possums as well as modeling potential foraging constraints due to animals moderating activity to avoid heat stress. We modeled the nutritional landscape for ringtails using a biogeochemical model that captured nutrient availability across study sites, informed by data on foliage chemistry, soil nutrients, geology, and climate. To identify likely drivers of population change, we used an open population model, which allows the estimation of vital rates, explicitly describing the dynamics of the population as a function of our indices of physiological stress and nutritional quality. Our case study provides mechanistic insight into the drivers of decline in rainforest ringtail possums. We highlight opportunities and challenges for applying this approach to other systems and describe how outputs from this framework can provide a solid foundation for conservation efforts.

2 | Materials and Methods

In this section, we provide an overview of our methodology as illustrated in Figure 1, with details in the “Extended Methodology” in [Supporting Information](#).

2.1 | Study System

The Australian Wet Tropics (Figure 2) is a tropical montane ecosystem, globally recognized for its significance owing to high endemism, evolutionary importance, and phylogenetic distinctiveness (Williams et al. 2016). Rainforest ringtail possums (family Pseudocheiridae), endemic to this bioregion, are medium-sized nocturnal marsupial folivores that primarily inhabit the canopy of upland rainforests. These species exhibit fragmented and geographically restricted ranges, likely influenced by historical rainforest extent fluctuations during the Pleistocene (Winter 1997). This study focused on two species of ringtail possums whose core populations overlap substantially, yet their overall distribution ranges differ markedly. The core of each species' range is centred between 700 and 1000 m elevation in the Atherton Tablelands, spanning -18° to -17° latitude. However, *Pseudochirops archeri* occupies a broader elevational and latitudinal range than the more range-restricted *Hemibelideus lemuroides* (Williams et al. 2010).

Previous research has explored the physiological limitations (Krockenberger et al. 2012), population trends (de la Fuente and Williams 2022), feeding ecology (Goudberg 1990; Jones et al. 2006), and drivers of spatial distribution (Kanowski et al. 2001) for both possum species. Despite gaps in our knowledge of their reproductive biology, field observations and data from related species suggest that rainforest ringtail possums reproduce during the dry season (April–November), typically producing a single offspring per year (Strahan 1995). Population monitoring of these species involved repeated annual counts of unmarked adult individuals across 32 study sites from 1992 to 2022. Although populations have been monitored for all four endemic ringtail possums in the region (de la Fuente and Williams 2022), physiological data were only available for *Pseudochirops archeri* and *Hemibelideus lemuroides*.

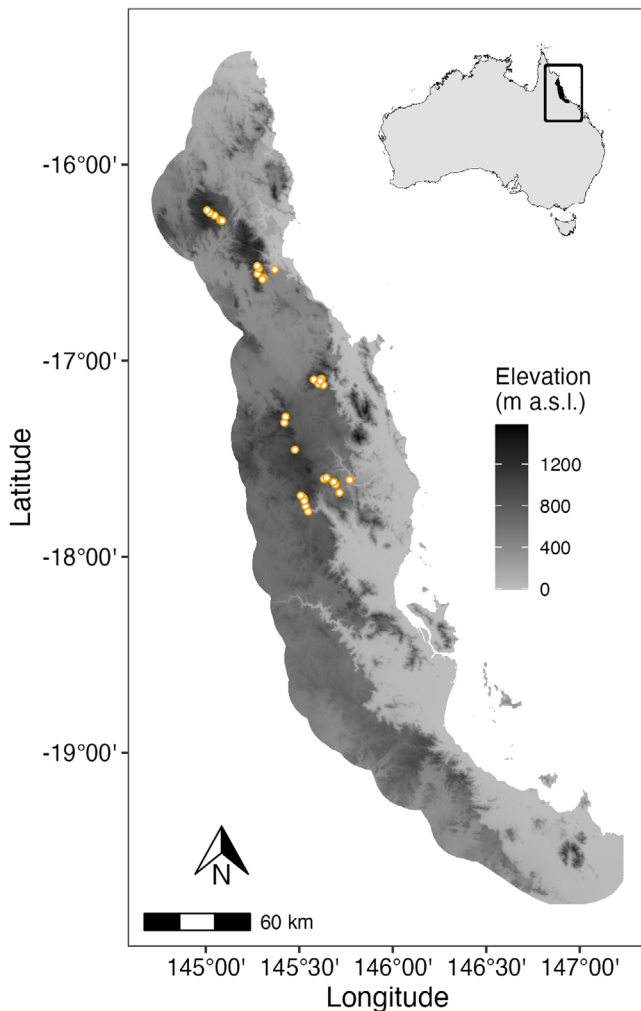


FIGURE 2 | The Australian Wet Tropics bioregion and its location in Australia. The gray colour palette represents the elevational gradient, with points indicating the locations of the long-term monitoring sites. Further details about the sites are provided in [Supporting Information](#). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

2.2 | Biophysical Ecology

Biophysical ecology employs models of microclimates, heat budgets, and thermoregulatory behaviour to describe animal performance by quantifying fluxes of energy and mass between organisms and their environment (Gates 1980).

2.2.1 | Microclimate Model

Hourly microclimate data were generated across the 32 study sites between 1992 and 2022 using the NicheMapR package (Kearney and Porter 2017), accounting for fine-grained topographic and mesoclimatic variability in the region (Storlie et al. 2013). We tested the accuracy of the microclimate model using an independent dataset consisting of hourly temperature measurements across four of our study sites between 2019 and 2020 (Leahy et al. 2022). This comparison indicated biologically sufficient levels of agreement (i.e., within 1°C; [Supporting Information](#): Extended Methodology).

Microclimate predictions were tailored to reflect the specific environmental conditions to which ringtail possums are exposed. For instance, we considered foraging animals to be exposed to a longwave radiation environment driven by estimated canopy temperature and included daytime den buffer effects for *H. lemuroides*. Den microclimate adjustments were based on hourly temperature data collected from 14 active possum dens monitored between 2007 and 2009, indicating a mean daytime buffer ranging between 0.25°C and 1.5°C cooler than outside ambient temperatures (Krockenberger [unpublished-a](#)). *P. archeri* does not den in tree hollows but instead spends daylight hours curled up on a branch in the canopy (Winter et al. 2008). Therefore, we assumed fully shaded microclimate exposure for *P. archeri* during the daytime.

2.2.2 | Animal Model

The thermoregulatory behaviour of ringtail possums was modeled using an endotherm-specific biophysical framework (Kearney et al. 2021), which incorporated species-specific physiological data (e.g., basal heat generation, maximum panting rate), morphological traits (e.g., body mass, fur properties), and behavioural adaptations (e.g., postural adjustments like uncurling rate) derived from experimental studies and museum specimens (Figure 1). We tested the performance of the animal model against observed metabolic data for the species (Krockenberger [unpublished-c](#); Krockenberger et al. 2012), demonstrating its ability to accurately replicate observed physiological responses under laboratory conditions ([Supporting Information](#): Extended Methodology).

2.2.3 | Activity Scenarios

Using the calibrated field microclimate data, we ran the animal model to predict physiological responses for ringtail possums across the 32 study sites for the period 1992–2022. Seven activity scenarios were designed to mimic the daily activity and feeding ecology of ringtail possums, resulting in a physiologically derived metric that quantified expected hourly activity based on biological and thermoregulatory constraints (Beale et al. 2023; Briscoe et al. 2022; Levy et al. 2016). These scenarios ranged from “resting” (i.e., non-active) to progressively more active states at 10-min intervals, each associated with a proportional increase in metabolic heat production, thus imposing higher thermal and hydric stress on the animals during more active states (Schmidt-Nielsen 1997). The overarching goal was to maximize nightly foraging potential [i.e., 5 h for *P. archeri* and 6 h for *H. lemuroides* (Goudberg 1990)] while minimizing water loss and avoiding overheating. Considering these constraints, possums were simulated to select the most optimal scenario each hour, resulting in an active-rest-active pattern that prompted rest during the daytime and whenever body temperature exceeded 0.5°C above their target core temperature, with target core temperatures based on laboratory studies of these two species (i.e., above 36.3°C for *P. archeri* and 37.8°C for *H. lemuroides*). This foraging activity framework was informed by feeding ecology studies of captive marsupial folivores under controlled temperature conditions, where the feeding rate gradually decreased with rising ambient

temperature (Beale et al. 2022). The integration of these activity scenarios allowed us to update the animal model to reflect field conditions. While other factors such as predation avoidance, intraspecific competition, territoriality, and human disturbance may influence foraging, they were not included in our model. Incorporating these highly variable ecological factors would require additional untested assumptions, potentially increasing rather than reducing the uncertainty of the results. We assessed the performance of the biophysical model under field conditions by corroborating physiological and behavioural predictions against field energetics data for ringtail possums (Goudberg 1990; Krockenberger unpublished-b), indicating that the biophysical model accurately captured field energy and water requirements for the species, with discrepancies between observed and predicted field metabolic rates of 0.43% for *P. archeri* (Observed: 383 KJ/day; Predicted: 381.37 KJ/day) and 2.28% for *H. lemuroides* (Observed: 546 KJ/day; Predicted: 533.55 KJ/day). This strong agreement between model predictions and empirical data supports the additional assumptions made to model physiological constraints on possums under field conditions.

2.2.4 | Rain Mitigation Effect on Water Loss

We incorporated mechanisms to mitigate water loss stress following rainfall events. Rainfall increases the availability of free water in the canopy of tropical rainforests, which strict folivores like ringtail possums can exploit by consuming wet foliage to replenish any water lost throughout the day. This compensatory mechanism was accounted for by temporarily balancing water loss to zero following significant rainfall events (i.e., daily rainfall exceeding 20 mm; [Supporting Information: Extended Methodology](#)).

2.2.5 | Physiological Stress Variables

Using the hourly field thermodynamics predicted by the biophysical model, we derived long- and short-term yearly physiological stress variables to quantify thermal stress, water loss, and foraging constraints for ringtail possums over the past 30 years, aligning with the temporal scale of our population dataset (Figure 1; Table 1). To evaluate the effects of climate change on physiological stress, we analyzed the rate of change in biophysical variables across spatial and temporal scales, fitting linear and curvilinear models. Spatial patterns captured changes in physiological stress along the elevational gradient, while temporal patterns reflected the annual rate of change from 1992 to 2022 across the species' distributions. Energy requirements were computed but were not considered further due to high correlations with other stress indices (see [Supporting Information: Extended Methodology](#)).

2.3 | Biogeochemical Dynamics

Foliage nitrogen (N; a proxy for protein) and its availability for mammalian folivores are crucial limiting factors that influence energy acquisition, individual fitness, population growth, and distribution (White 2012). We defined the

nutritional landscape for ringtail possums using metrics that captured foliage quality, including total N, available N, and the effect of tannins on N digestibility (de la Fuente et al. 2024; DeGabriel et al. 2008; Wallis et al. 2012). Chemical assays were performed on canopy foliage samples collected across 25 of the 32 study sites for three rainforest tree species that represent some of the main browse species in ringtail possums' diets (Goudberg 1990; Jones et al. 2006). Soil was collected across the same sites to consider potential bottom-up effects on nutrient cycling.

To capture foliage quality across the unsampled sites, we developed a Bayesian hierarchical biogeochemical model that described the spatial pattern in foliage nutritional chemistry as a function of climate, geology, and soil nutrients (Figure 1). This approach allowed a robust stochastic imputation of soil and foliage chemistry across unsampled sites based on the overarching biogeochemical dynamics (de la Fuente et al. 2024). The spatial variability in nutritional value for ringtail possums was approximated based on the maximum total N and available N and the minimum tannin effect at each site, as we assumed that ringtail possums selectively forage in trees that maximize diet quality while minimizing metabolic costs.

2.4 | Population Dynamics

To unravel the mechanisms underlying changes in abundance over space and time, we implemented a Bayesian hierarchical population model that explicitly describes the processes governing population dynamics (Dail and Madsen 2011). These models facilitate the estimation of vital rates such as survival and recruitment, as well as population growth and abundance, using simple counts of unmarked individuals replicated across space and time. Temporal fluctuation in abundance at a particular location is characterized by the sum of survivors from the previous year and the number of new individuals at that site. Therefore, apparent survival encompasses mortality and emigration, while recruitment includes birth and immigration.

Our population model, based on the approach outlined by Bellier et al. (2016), integrates density dependence and spatiotemporal covariates into the estimation of vital rates. This open population model allows exploration of the effects of physiological constraints and foliage nutritional quality on population dynamics by integrating biogeochemical and biophysical processes (Figure 1). A further advantage of this hierarchical model structure is that, by using repeat surveys conducted within the same year to model detection probability, we were able to explicitly account for factors that affect observed survey counts when estimating true site abundances. We modeled spatial variation in the initial population in 1992 as a function of elevation and metrics of foliage quality, while spatiotemporal changes in recruitment and survival for the period 1993–2022 were modeled as functions of physiological stress variables. The effects of density dependence on population dynamics were tested following the model selection outlined in Bellier et al. (2018), with results suggesting that density dependence was acting only on recruitment for both species. Detection probability was modeled as a response to

TABLE 1 | Description of physiological stress and performance variables derived from the biophysical model that captures thermal, water-loss, and foraging constraints.

Stress/ performance category	Scale	Definition	Units	Variable
Thermal	Long-term	Cumulative hourly stress in a year. Thermal stress was defined as hours when predicted body temperature exceeded a threshold (0.5°C above the species' target core temperature), with stress values indicating the amount of heat that surpassed this core temperature threshold. Stress values were summed annually	°C·h	Thermal dosage
Thermal	Short-term	Cumulative hourly stress during the highest intensity extreme heatwave recorded in a year. An extreme thermal event was defined as five or more consecutive hours of thermal stress, as proposed by Krockenberger et al. (2012)	°C·h	Thermal intensity
Water loss	Long-term	Percentage of the year in which the animal is significantly water stressed, with water stress defined as hourly evaporative water loss greater than the 90th percentile of all values (across all sites and years)	%	Long-term evaporative water loss (EWL)
Water loss	Short-term	Maximum cumulative 4-days water loss	g of H ₂ O	Short-term EWL
Foraging	Long-term	Percentage of nights in summer with a cumulative foraging time above 80% of the maximum foraging potential	%	Long-term foraging performance
Foraging	Short-term	Minimum cumulative 2-days foraging time. Values were scaled using the species' potential maximum foraging time to offer a comparable metric between species	% of potential maximum	Short-term foraging performance

Note: Long-term variables were calculated by summarising annual hourly data (cumulative/chronic impacts), while short-term variables were designed to capture acute stress events that occurred over hours to days. The water stress metrics already incorporate rain mitigation effects.

survey effort, reflected by the number of observers in each survey, as well as the expected levels of animal activity during the survey (i.e., potential activity in our model) predicted for the exact location and night of each survey using the biophysical model described above.

In Bayesian hierarchical models, the same observed data can arise from different combinations of latent processes, which makes model selection challenging (Hooten and Hobbs 2015). Commonly used approaches such as Leave-One-Out Cross-Validation and the Widely Applicable Information Criterion (WAIC) cannot readily be applied to models like ours due to the high interdependencies among latent states, which prevent independent evaluation of likelihood components (Hooten and Hobbs 2015; Vehtari et al. 2017). To identify the most parsimonious population models, we followed the approach of Bellier et al. (2018), basing model selection on posterior stability and ecological realism. This involved a five-step sequential selection process, where we constructed all potential candidate models and assessed parameter stability across them (Supporting Information: Extended Methodology). Our approach ensured that key variables consistently contributed to inference while minimizing artefacts from interdependencies.

It also allowed us to validate variable importance and detect confounded predictors (see Supporting Information: Extended Methodology). All models were fitted in JAGS using uninformative priors (Supporting Information: Extended Methodology).

3 | Results

3.1 | Climate Change Intensifies Physiological Stress

Species' physiological responses varied strongly across elevation. Thermal stress intensity (short-term) and dosage (long-term) significantly decreased with elevation, while associated foraging performance showed a strong increase along the same gradient (Figure 3). However, *P. archeri* was more susceptible to thermal physiological stress than *H. lemuroides* under the same environmental conditions across both space and time (Figure 3). For instance, long-term cumulative yearly thermal stress increased towards lower elevations at an average rate of $0.77^{\circ}\text{C} \pm 0.25^{\circ}\text{C}\cdot\text{h}$ per 100m for *H. lemuroides*, whereas it increased at a rate of $29.62^{\circ}\text{C} \pm 6.01^{\circ}\text{C}\cdot\text{h}$ for *P. archeri*, indicating

that *P. archeri* is under severe thermal stress at lower elevations. Interestingly, constraints on foraging activity were more similar between species, with *H. lemuroides* showing an average increase in annual foraging performance of $5.46\% \pm 0.84\%$ per 100m increase in elevation, compared to the $8.81\% \pm 0.76\%$ for *P. archeri* (Supporting Information: Extended Results). This could indicate that thermal stress for *H. lemuroides* was manifested through its effect on foraging activity rather than direct overheating. Lastly, results related to water stress suggested a positive linear correlation between evaporative water loss and elevation (Figure 3A). This pattern aligns with the spatial distribution of upland rainforest, which extends westward into drier regions, influencing water loss patterns across the elevational gradient (Figure 2).

Since 1992, physiological stress in both ringtail species has varied over time, with an overall trend of increasing stress in recent years (Figure 3B). Thermal stress exhibited a curvilinear pattern, with a decrease in heat stress in the early years followed by an increase in recent decades, mirroring observed heatwave patterns in the region (Bureau of Meteorology 2023; de la Fuente and Williams 2022). Conversely, short-term foraging constraints showed an inverse response, suggesting higher foraging activity in the first half of the time series, followed by a decrease in short-term foraging performance in later years. The temporal pattern in long-term foraging performance exhibited a linear decline over time, with approximately $1\% \pm 0.48\%$ decrease in foraging performance every 10 years across ringtail species (Supporting Information: Extended Results). This translates to an average of 5.6 extra nights in which the animal achieved less than 80% of their foraging potential per summer across the species distribution in 2022 compared to 1992. The effects of climate change suggested an overall escalation in water loss stress over time. For *P. archeri*, water stress showed a curvilinear pattern in short-term water loss similar to that observed for thermal stress, while long-term annual stress followed a linear temporal increase. In contrast, evaporative water loss showed a marginal temporal response for *H. lemuroides*, likely reflecting the lower thermoregulatory cost associated with increased temperature for the species derived from a higher target core temperature (37.3°C compared to 35.8°C for *P. archeri*).

3.2 | Geology Is Associated With Foliage Quality for Ringtail Possums

Foliar nitrogen concentration of the trees on which ringtails forage was strongly influenced by geology. After accounting for climate effects, models indicated that trees growing in basaltic soils exhibited higher levels of total foliar nitrogen compared to those in granite and rhyolite soils. Specifically, the maximum foliar nitrogen concentration of trees in basalt soil was $35.46\% \pm 0.06\%$ (mean \pm standard deviation) higher than that of trees in granite sites and $34.62\% \pm 0.1\%$ higher than that in rhyolite sites. This pattern was consistent across all sampled tree species. The processes governing the variability in foliage and soil nutrients across the landscape are further explored in de la Fuente et al. (2024) and Supporting Information.

3.3 | Physiological Stress Explains Long-Term Population Dynamics

The impact of climate change on ringtail possum populations was captured by the combined effect of habitat quality (defined by elevation and foliage nutritional chemistry), physiological performance, and the influence of density dependence on recruitment. The spatial distribution of initial abundance was positively correlated with elevation for both species (Figure 4), indicating that ringtail possum populations are, on average, larger in cooler upland rainforest compared to habitats found at lower elevations. After accounting for the effect of elevation, the abundance of *H. lemuroides* was positively correlated with total foliar nitrogen (Figure 4B), suggesting that the species finds its optimal habitat in high-elevational rainforests with basaltic soils, where temperature is moderate and foliage nutritional quality is high (Figure 5).

Spatiotemporal changes in ringtail possum populations were explained by the impact of climate-induced physiological stress on vital rates. For the more broadly distributed *P. archeri*, changes in survival were negatively correlated with thermal intensity and long-term water loss stress, while recruitment was positively influenced by long-term foraging performance (Figure 4A). Consequently, substantial declines in *P. archeri* populations are predicted in the years following extreme summers, where overheating and dehydration could severely constrain survival, and reduced foraging activity could lead to decreased recruitment. For the upland-restricted *H. lemuroides*, the impact of climate change on population dynamics was primarily expressed through the physiological limitations imposed on foraging performance. Population declines for this species are also expected following extreme summers, where heatwaves could threaten survival by limiting short-term foraging time, and a reduction in long-term foraging performance in hot years could limit the recruitment rate (Figure 4B). We detected a density-dependence constraint in recruitment for both species (Figure 4), suggesting potential limitations associated with resource availability across the landscape.

Ringtail possum detectability was significantly influenced by variations in survey effort and potential activity (Figure 4). Detection probability was positively associated with the number of surveyors for both species. However, survey effort had a greater influence on the detectability of the more cryptic *P. archeri* compared to *H. lemuroides*. Potential activity linked to physiological factors was the strongest predictor of detectability for *H. lemuroides* (Figure 4B), consistent with the importance of foraging constraints for population dynamics. This indicates that detection probability for this species increased on cooler nights due to heightened foraging activity. These detectability findings bolster confidence in the biophysical model's performance, demonstrating its ability to accurately predict activity patterns that correspond with survey-specific detection probabilities.

4 | Discussion

Our study demonstrates new ways to integrate nutritional and eco-physiological constraints with population dynamics to

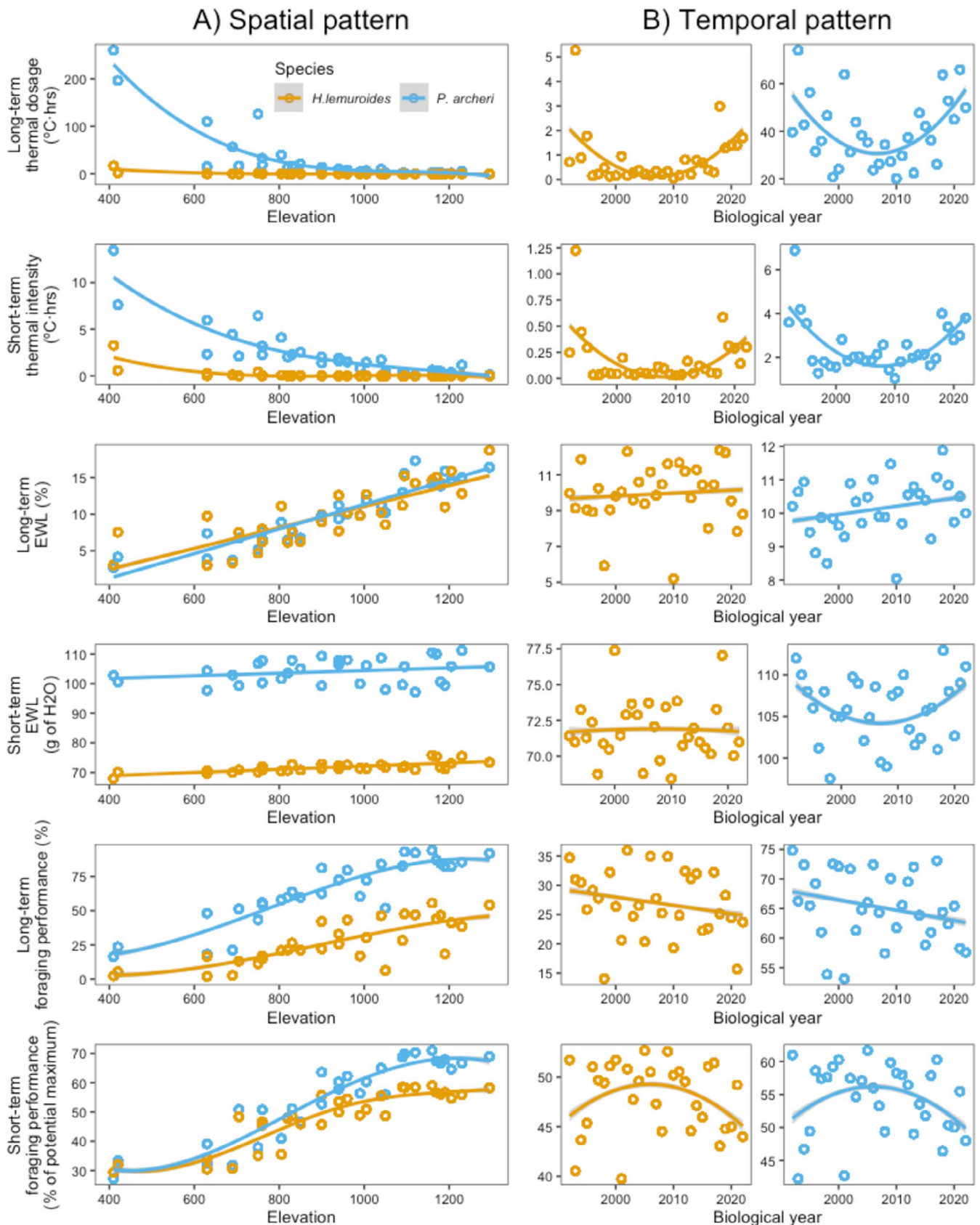
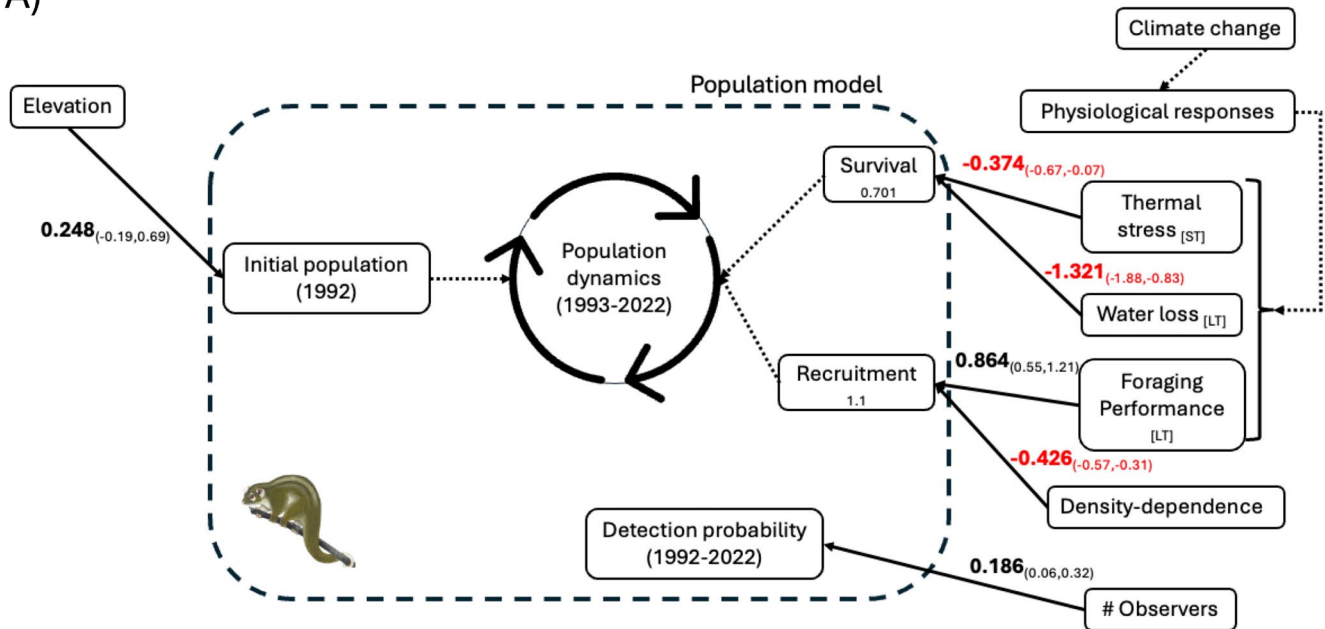


FIGURE 3 | Physiological stress of ringtail possums *P. archeri* (blue) and *H. lemuroides* (orange) across space and time. Spatial patterns (A) illustrate physiological response changes along the elevational gradient (averaged across years), while temporal patterns (B) show the physiological response change from 1992 to 2022 (averaged across sites). Biophysical variables are detailed in Table 1. Biological year refers to yearly time increments used in the population model. The year starts in April (i.e., right before the breeding season) to better capture the cumulative pressure of extreme summer conditions (from December to March) on population dynamics. EWL, evaporative water loss.

A)

Species: *Pseudochirops archeri*

B)

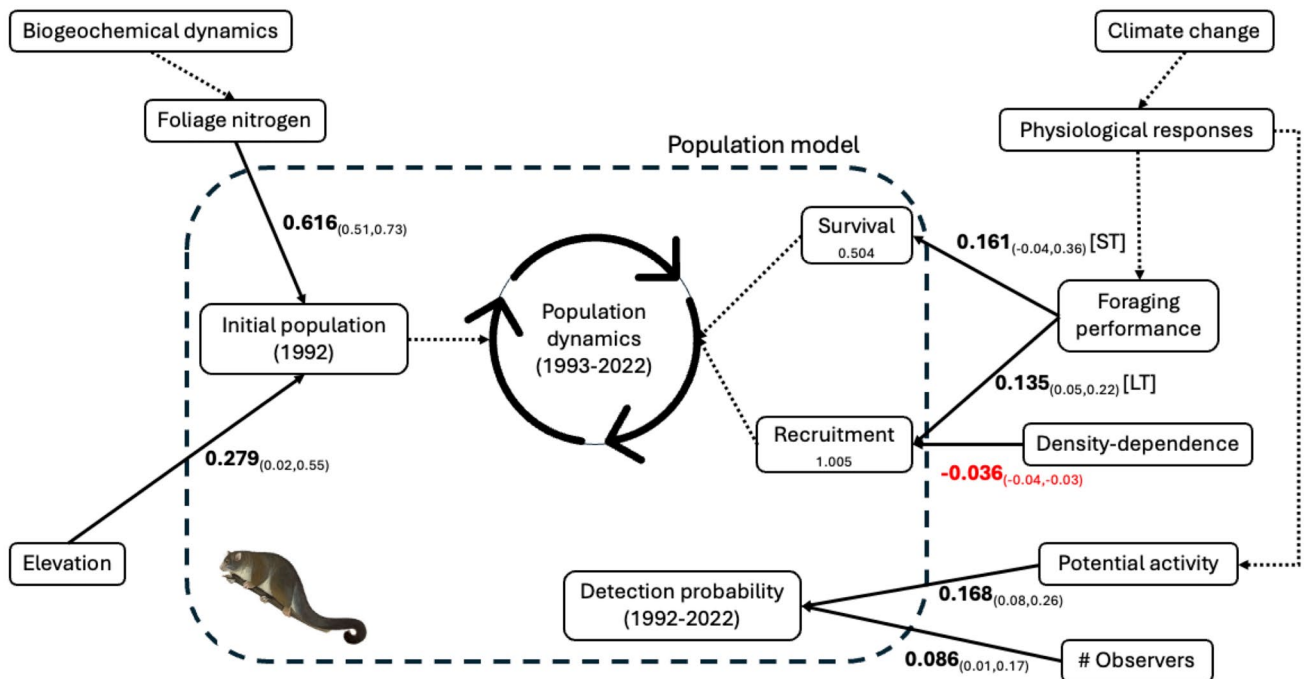
Species: *Hemibelideus lemuroides*

FIGURE 4 | Conceptual summary of population dynamics for ringtail possums *P. archeri* (A), and *H. lemuroides* (B). Dotted lines represent the processes that led to the factors informing population dynamics. Solid lines represent the direct effect of different predictors on population processes. Values in bold represent the mean effect for those factors, with black values indicating positive correlations while red values indicate negative effects. Subscripts show the credible interval, describing the uncertainty around the mean effect, indicating the 5.5th and 94.5th percentiles of the sorted posterior samples. Initials following the subscript refer to the temporal scale of the variable influencing population parameters (LT, long-term; ST, short-term). Values under survival and recruitment represent the estimated baseline rates under average conditions. For a detailed quantitative representation of the partial effects of each predictor on abundance, survival, recruitment, and detection, see the posterior predictive partial dependence effect plots in [Supporting Information](#) (Extended Results; Figures ER1 and ER2).

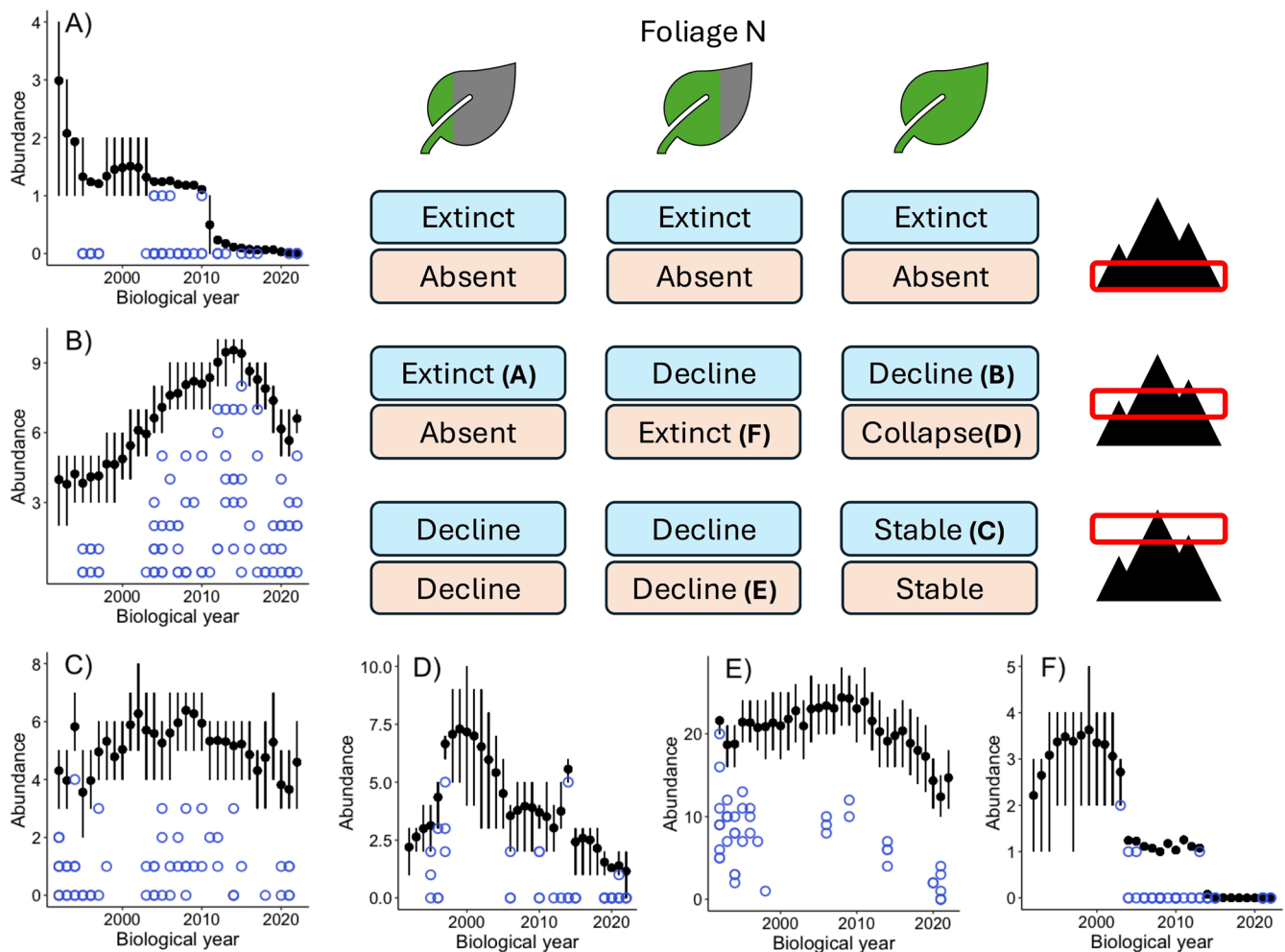


FIGURE 5 | Summary of population trajectories for *P. archeri* (blue; A–C) and *H. lemuroides* (orange; D–F). Plots (A–F) display the predicted true abundance (black) and raw count data uncorrected for detection probability (blue) for selected examples from the elevation and foliage nitrogen matrix. Biological year refers to the adjusted temporal treatment of the population model. The results are presented in a matrix with elevation and foliage nitrogen as its axes, illustrating the interaction between these factors and their influence on population dynamics. Population trajectories are classified as: Stable (minor fluctuations without long-term declines), Decline (gradual or recent reduction with potential for recovery), Collapse (severe reductions to critically low numbers, limiting recovery potential), and Extinct (previously present but now absent). Elevation categories range between 400 and 700 (low), 800 and 1100 (mid), and 1100 and 1350 (high). Foliage nitrogen concentration is divided into low concentration (below the 33rd percentile), mid concentration (between the 33rd and 66th percentile), and high concentration (above the 66th percentile).

better understand how and why animal populations decline under climate change. This biophysically informed population model produces specific and testable hypotheses regarding some of the mechanisms driving species declines, offering deeper insights into ecological responses to climate change than is possible with physiologically implicit approaches. Our application of this integrated approach to rainforest ringtail possums demonstrated that even functionally similar species can respond very differently to the same habitat conditions, emphasizing the importance of capturing these nuanced dynamics for effective management. Furthermore, the model's ability to predict physiological responses extends to explaining survey-level detection patterns, providing biologically meaningful insights into species–environment interactions at very fine scales. The generality of the biophysical ecology principles underpinning the model makes this approach

broadly applicable to any species for which detailed, long-term population data are available.

4.1 | Climate Change Reduces Species Fitness

Our findings highlight how climate change can disrupt physiological performance and life history responses in mammalian folivores, directly impacting their survival and recruitment. Short-term extreme events significantly constrain survival, likely due to acute physiological stress leading to direct mortality, particularly in individuals already near their physiological limits. In contrast, long-term seasonal stress accumulates over time, likely affecting body condition, energy reserves, and ultimately reproductive success, thereby influencing recruitment. This distinction illustrates the multifaceted nature of climate

stressors on population dynamics, where different timescales of stress exposure drive distinct demographic consequences (Harris et al. 2018). Our results provide evidence of how rapid climatic changes are altering the ecological stability of vulnerable species, reflecting broader patterns of climate impacts on wildlife globally (Parmesan et al. 2000).

For the upland-restricted *H. lemuroides*, survival was particularly constrained by limited foraging time, indicating that thermoregulatory constraints over just two consecutive nights could prove fatal, likely due to the species' low energy reserves (Rübsamen et al. 1984). This is consistent with previous studies that suggest that climate-induced limitations on foraging activity may lead to fatal outcomes in marsupial folivores by rapidly depleting energy and water reserves (Beale et al. 2022, 2023; Wagner et al. 2020; Youngentob et al. 2021).

For the more widely distributed *P. archeri*, overheating and dehydration were major factors limiting survival, in line with experimental studies (Krockenberger et al. 2012). During heatwaves, *P. archeri* employs facultative heterothermy, allowing body temperature to rise to minimize evaporative water loss (Krockenberger et al. 2012). While this strategy allows *P. archeri* to cope with extreme heat for short durations, prolonged exposure requires substantial evaporative cooling to regulate body temperature, thereby risking dehydration. Our findings confirm that heat stress lasting over 5 h without immediate access to free water can significantly reduce survival (Krockenberger et al. 2012), highlighting how physiological constraints linked to thermoregulation directly impact population dynamics.

Climate change impacts on recruitment showed similar trends for both species, with the number of new recruits strongly depending on foraging performance in the preceding year. Hot summers reduced nutrient acquisition, subsequently lowering reproductive success. These results are in line with earlier research that connects reduced nutrient availability to declines in recruitment among marsupial folivores (Beale et al. 2018; DeGabriel et al. 2009; Kearney, Wintle, et al. 2010). For example, in the related species *Petauroides volans*, protein intake has been identified as a key limiting factor for milk production in the Wet Tropics, significantly constraining modeled breeding potential (Kearney, Wintle, et al. 2010).

While direct overheating was not the primary physiological constraint for *H. lemuroides*, its elevational restriction appears to be closely tied to its inability to forage effectively in warmer environments. Unlike *P. archeri*, which can tolerate short-term heat stress through facultative heterothermy, *H. lemuroides* faces severe foraging limitations when exposed to even mild thermal stress. The species' strict folivorous diet and high energy demands make continuous foraging essential for both survival and recruitment, and our results suggest that reduced foraging time at lower elevations may limit its distribution. This illustrates how climate change impacts are not always driven by direct overheating but can emerge through behavioral and ecological constraints that ultimately shape population persistence.

Population density influenced recruitment in both species; increased animal density decreased recruitment, suggesting the presence of limiting factors in the environment. For *H.*

lemuroides, this limitation could be associated with den availability (Kanowski 1999), whereas for *P. archeri*, territoriality might restrict resource access across the landscape (Krockenberger unpublished-d). These observations are consistent with previous findings that suggest irregular resource distribution can affect reproductive success among territorial marsupial folivores (DeGabriel et al. 2009; Youngentob et al. 2012).

4.2 | The Population Collapse of Ringtail Possums

Climate change is fundamentally altering species distributions by differentially affecting populations across their range, particularly along elevational gradients (Chen et al. 2011; Urban 2018). Our results demonstrated that physiological stress among rainforest ringtail possums is strongly influenced by elevated temperatures, suggesting that the impact of warming is amplified at lower elevations, where temperatures are higher, and heatwaves are more extreme and frequent. Therefore, the fate of ringtail possum populations is tightly linked to their position along the elevational gradient, with warming imposing biologically limiting stress at the lower range of their distributions, resulting in local extinctions observed at sites below 750 m for *H. lemuroides* and 600 m for *P. archeri* (Figure 5). Thermoregulatory constraints at lower elevations could be exacerbated in areas of low nutritional quality, where local extinctions of *H. lemuroides* have been observed at sites as high as 850 m. This finding underscores the crucial role of the nutritional landscape in shaping population dynamics (Au et al. 2019; DeGabriel et al. 2009; Marsh et al. 2014; Moore et al. 2004). Even at the core of their distribution, extreme summer conditions have led to increased physiological stress, resulting in significant declines over recent decades. However, populations persist in relatively healthy numbers, compared to 1992, in optimal habitats characterized by high-elevation rainforests with high nutritional value (Figure 5). This emphasizes the critical role of protecting high-quality habitats as refuges for species vulnerable to climatic extremes.

The physiological responses contributing to the collapse of rainforest ringtail possums follow a distinct curvilinear pattern, characterized by a decline in stress from 1992 to 2010, followed by a substantial increase from 2010 to 2022 (Figure 3). This trend closely mirrors the changes in heatwave frequency in the region and aligns with documented population declines in the species (de la Fuente and Williams 2022). By directly linking these physiological responses to climate extremes, our findings offer a mechanistic explanation for the rapid population collapse of ringtail possums in the Australian Wet Tropics. This connection highlights the critical role of physiological stress in driving population declines and underscores the importance of understanding thermal physiology and nutritional landscapes under escalating climate pressures.

4.3 | A Foundation to Guide Conservation Efforts

This study provides a critical foundation for guiding conservation efforts by uncovering the mechanisms driving climate-induced ecological responses in wild populations. Understanding the specific causes of population declines is crucial in conservation biology as it allows for the design of targeted and effective

interventions. For instance, provision of resources (food or water) and habitat manipulation (artificial dens) are two conservation interventions previously used for species impacted by climate change, including arboreal folivores in Australia (Felton et al. 2022; Gracanic et al. 2025; Mason and Hartog 2024; Mella et al. 2019). Of these options, our results provide support for exploring enhanced resource availability (water for *P. archeri* and nutritional quality for both species), especially when these resources are most limiting at the end of the dry season. Model outputs indicate where these actions are likely to have the most impact—populations at lower elevations and in areas with low foliage nitrogen. While resource provision is challenging, artificial water stations have already been successfully trialled for another arboreal folivore, the koala, following studies that identified water requirements as a key constraint on inland populations (Briscoe et al. 2016; Mella et al. 2019). While our model can be used to help refine which management actions are likely to be effective, it is essential to evaluate their feasibility and potential ecological consequences before implementing such interventions. For example, altering resource availability could have cascading effects on other aspects of ecosystem functionality. Alongside these considerations and field trials, our biophysically informed population model could be used to simulate different management scenarios and project population trajectories under various intervention strategies to evaluate the short- and long-term impacts of these decisions.

4.4 | Limitations and Future Directions

There are currently several challenges that limit broader application of the integrated approach we have presented. First, biophysical models require substantial data for accurate parameterization (Briscoe et al. 2023). Although obtaining such detailed data can be resource-intensive, the availability of required trait information is steadily increasing through experimental studies, online databases, and museum specimens (Riddell et al. 2023). Further coordinated data collection efforts and investment in developing robust trait imputation methods could rapidly enhance our ability to apply these methods.

Second, available nutritional data often capture resource quality at coarse spatial or temporal scales. Long-term, fine-scale spatiotemporal data are often unavailable, constraining the inclusion of such dynamics into models. In addition, we rarely have a complete understanding of every foliar chemical constituent that could influence food intake and an herbivore's ability to meet its energy requirements in any plant–animal system. As a result, models may only partially represent the impact of nutrient availability on population dynamics, missing key variations across both space and time. In our study, foliage nutritional data were derived from samples collected across several rainforest tree species between 2021 and 2022. While this provided valuable insights into spatial variability in nutrient availability for ringtail possums, it did not capture potential long-term changes in foliage nutritional quality, which have been documented in other tropical rainforests (Rothman et al. 2015). Such temporal changes in leaf chemistry could have significant implications for the population dynamics of marsupial folivores (Beale et al. 2018).

Lastly, despite their importance for studying species responses to environmental change (Parmesan 2006), long-term population monitoring programs across broad spatial scales are relatively rare and taxonomically biased (Moussy et al. 2022). While our dataset (32 sites and 31 years) was relatively large for an ecological study of this nature, data limitations still meant that we were unable to explore more complex models (e.g., that included interactions between foliage quality and foraging constraints) or set aside data for model testing, the gold-standard approach to model evaluation (Hooten and Hobbs 2015). Coupling greater investment in well-designed and maintained monitoring programs with modeling approaches that can elucidate information on both species' trends and the underlying mechanisms will be crucial to effectively managing species' responses to climate change.

4.5 | Conclusions

This study provides new insights into the mechanisms driving climate-related ecological responses in two species of ringtail possums. We have shown that climate change fundamentally alters population dynamics by intensifying physiological stress, leading to decreased survival and recruitment. Specifically, the effects of overheating, dehydration, and reduced foraging performance have been identified as key drivers of population declines. These physiological stresses are exacerbated at lower elevations, where they may reach biologically limiting levels, resulting in local extinctions. However, targeted intervention based on our findings could improve conservation outcomes for these species. By highlighting the mechanisms underlying these population declines, the approach we have demonstrated creates a robust framework for evaluating potential interventions. With appropriate data, this framework could be broadly applied to guide conservation efforts for vulnerable species, ensuring that actions are both effective and efficient in mitigating the impacts of climate change.

Author Contributions

Alejandro de la Fuente: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, validation, visualization, writing – original draft. **Natalie J. Briscoe:** conceptualization, formal analysis, investigation, methodology, resources, software, validation, writing – review and editing. **Michael R. Kearney:** conceptualization, formal analysis, methodology, software, validation, writing – review and editing. **Stephen E. Williams:** funding acquisition, resources, supervision. **Kara N. Youngentob:** formal analysis, methodology, resources, writing – review and editing. **Karen J. Marsh:** methodology, resources, writing – review and editing. **Lucas A. Cernusak:** supervision, validation, writing – review and editing. **Lily Leahy:** resources, writing – review and editing. **Johan Larson:** methodology, resources. **Andrew K. Krockenberger:** conceptualization, funding acquisition, investigation, methodology, resources, supervision.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and code that support the findings of this study are openly available in Dryad at <https://doi.org/10.5061/dryad.fxpnvx13n>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.