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Author for correspondence:
V. Gjoni
e-mail: vojsava.gjoni@unipa.it

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Metabolic scaling of an invasive mussel depends on temperature and chemical cues from an invasive predator

V. Gjoni[1,2], G. Marchessaux[1,2], D. S. Glazier[3], J. S. Wesner[4], M. Bosch-Belmar[1,2], F. P. Mancuso[1,2], M. F. Tantillo[1,2], N. Marsiglia[1,2] and G. Sarà[1,2]

[1]Department of Earth and Marine Science (DiSTeM), University of Palermo, Palermo, Italy
[2]NBFC, National Biodiversity Future Center, Palermo, Italy
[3]Department of Biology, Juniata College, Huntingdon, PA, USA
[4]Department of Biology, University of South Dakota, Vermillion, SD, USA

VG, 0000-0003-1740-6093; DSG, 0000-0001-7164-1823; GS, 0000-0002-7658-5274

Metabolism drives various biological processes, potentially influencing the ecological success and evolutionary fitness of species. Understanding diverse metabolic rates is fundamental in biology. Mechanisms underlying adaptation to factors like temperature and predation pressure remain unclear. Our study explored the role of temperature and predation pressure in shaping the metabolic scaling of an invasive mussel species (*Brachidontes pharaonis*). Specifically, we performed laboratory-based experiments to assess the effects of phenotypic plasticity on the metabolic scaling by exposing the mussels to water conditions with and without predator cues from another invasive species (the blue crab, *Callinectes sapidus*) across various temperature regimes. We found that temperature effects on metabolic scaling of the invasive mussels are mediated by the presence of chemical cues of an invasive predator, the blue crab. Investigating temperature–predator interactions underscores the importance of studying the ecological effects of global warming. Our research advances our understanding of how environmental factors jointly impact physiological processes.

1. Introduction

Temperature plays a crucial role in influencing the rates of various physiological and ecological processes [1,2]. Therefore, many studies of non-invasive species have focused on how temperature affects two major organismal traits, body size and metabolic rate [1,3–5]. The Metabolic Theory of Ecology (MTE) predicts that metabolic rates increase exponentially with temperature, regardless of an organism's body size. This implies that the metabolic scaling slope should remain constant across different environmental temperature gradients. However, deviations from the putative universal slope of MTE have been reported. Experimental studies have shown size-dependent responses of the metabolism as temperature increases, thus altering the slope of the metabolic scaling [6–10]. These temperature-induced deviations from the expected metabolic scaling patterns can partly be explained by the metabolic-level boundaries hypothesis (MLBH); reviewed by Glazier and Killen *et al*. [6,9,10]. The MLBH posits that as temperature increases, the influence of surface-area-related metabolic processes increases relative to that of volume-related processes, thus causing a shift in metabolic scaling slope from a maximum of 1 to a minimum of 2/3 in isomorphic organisms. Nevertheless, very little is known about the metabolic scaling of non-indigenous species (hereafter NIS) and even less about how it may be affected by environmental factors.

While it is well-established that temperature can exert immediate phenotypic effects on the mass-specific metabolic rate of certain organisms [6,8,9,11], the organism's capacity for physiological adjustments in shaping metabolic scaling in response to predation risk is largely unexplored [12,13]. Indeed, predation risk is well known for its significant influence on the phenotypic expression of various traits in prey organisms, such as morphological features, behavioural patterns and life-history strategies [14–17]. Moreover, experiments have demonstrated that predation risk can modify the influence of temperature on prey phenotypes, including behaviour and life-history traits [18–25]. The presence of non-native species can further induce changes in the behaviour, morphology or life history traits of native species, thereby affecting their interactions with both predators and prey. Nevertheless, the phenotypically plastic effects of temperature and predators, or their cues, on metabolic scaling have received limited attention in non-invasive species [26,27] and are unexplored in non-native species.

The biological invasion of marine species is one of the main indirect consequences of global warming [28,29]. The spread of NIS around the world [30,31] is known as the most detrimental biotic driver affecting autochthonous biodiversity in numerous ecosystems worldwide [29,32–34]. The mussel, *Brachidontes pharaonis*, exhibits typical NIS characteristics in tolerating a wide range of temperatures (9–31°C) [35]. Similarly, the blue crab, *Callinectes sapidus*, lives across habitats spanning 3–40°C [36]. By taking advantage of global warming, the ecological and economic impacts of these species are increasing owing to their ability to adapt to non-native habitats. The impact of global warming on the survival of non-native species is a major issue for ecosystem conservation. Therefore, it is important to understand how and why increasing temperature affects physiological adaptations of non-native species to non-native habitats.

The purpose of our study was to investigate how temperature and predation cues from an invasive blue crab *C. sapidus* may interact to affect ontogenetic metabolic scaling of the invasive mussel *B. pharaonis*, a common prey organism in a Mediterranean marine lagoon. Using this approach allowed us to define the temperature-induced metabolic response of an invasive prey to predation risk by another invasive species. To our knowledge, our study is the first to explore how the metabolic scaling of an invasive species may be jointly affected by an abiotic factor (temperature) and biotic factor (chemical cues from an invasive predator), thereby providing important physiological information needed to predict the distribution and ecological interactions of these invasive species in the Mediterranean Sea.

2. Material and methods

(a) Model systems

Our study used invasive mussels (*B. pharaonis*) that were collected from the lagoon Stagnone of Marsala in Italy. Once collected, *B. pharaonis* specimens were immediately placed in a controlled room and acclimated for at least 7 days at a constant temperature also used during the respiration measurements. The experimental temperatures were within the range encountered naturally by each species in Mediterranean Sea water. Furthermore, blue crabs (*C. sapidus*) from the same lagoon were used as a proxy for predation pressure.

The experiment involved a full-factorial design divided into the following six groups: three levels of temperature (13, 20 and 27°C) and two levels of predation regime (absence versus presence of chemical cues). Each group exposed (or not) to chemical cues of blue crabs was divided into three groups (size-based selected) exposed to three different water temperatures. Before respiration measurements, mussels were fasted for 24 h in water with or without crab cues. Water with crab cues was prepared by placing two crabs (10 cm) in each tank with 10 l of water for 24 h (figure 1).

(b) Respirometry

Individual respiration rate (RR; μl O_2 h^{-1}) was used as a proxy for metabolic rate [35,36]. After exposure to an experimental temperature in water with or without crab cues, *B. pharaonis* specimens were individually introduced into respirometric chambers (20 ml for small organisms and 130 ml for the biggest), containing filtered (Whatman GF/C, 0.45 mm) air-saturated seawater (44 psu) and an individual stirring device to mix the water [40]. Chambers were placed inside thermostatically controlled baths (Grant Optima TX150 and TECO 150 chiller systems) to guarantee a stable temperature during the measurements. PyroScience system (Firesting O_2 optode sensors) was used to measure the oxygen concentration at the highest temporal scale resolution (measuring every second for 1.5 h). RR was calculated using the equation given below (according to Sarà *et al.* [41]):

$$RR = (Ct_0 - Ct_1)V(t_1 - t_0)^{-1}$$

where 'Ct_0' is the oxygen concentration at the beginning of the measurement, 'Ct_1' is the oxygen concentration at the end of the measurement and 'V' is the volume of water in the respirometric chamber. Respiration measurements were individually performed for each organism. In this way, despite sharing the same exposure conditions, each organism's respiratory responses were measured independently. Control measurements of oxygen concentration were also taken. After RR measurements, wet weight (mg) of all organisms was recorded as a proxy for the body size.

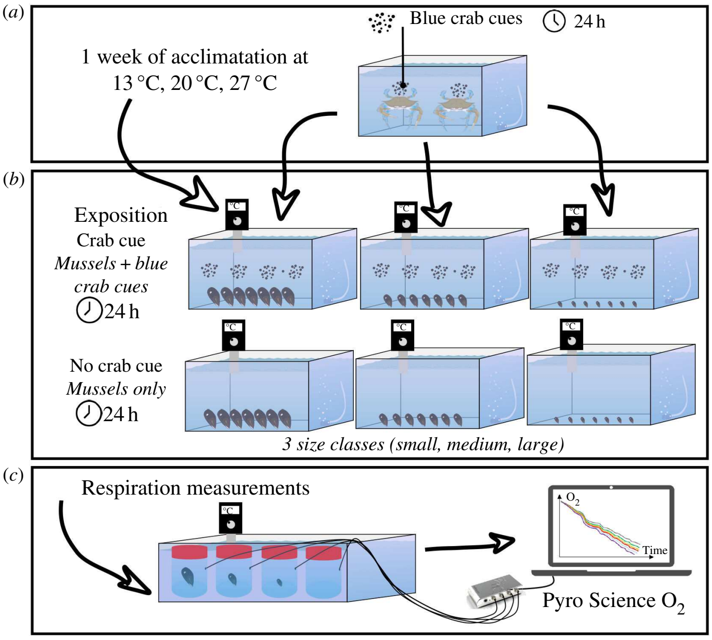

Figure 1. Blue crabs were captured using a hand net, and mussels were collected using a mussel rake. (*a*) In the laboratory, blue crabs were placed in a 15 l aquarium with two crabs per tank. (*b*) In each tank, the mussels were categorized into three size classes (small: <1 cm; median: 1–2.5 cm; large: >2.5 cm), and each size class was placed in 15 l aquariums equipped with an air pump (30 organisms per aquarium). For mussel acclimation, the temperature was gradually decreased or increased by 1°C per hour, and the mussels were acclimatized for one week at the target temperature (following Hicks & McMahon [37]). The same acclimation process was applied to the blue crab cues. Chemical cues exposure was conducted uniformly for 24 h under identical conditions, where the crabs (10 cm carapace width) were not fed during this process (following Cheung *et al*. and Côté & Jelnikar [38,39]). (*c*) Respiration measurements were individually performed for each organism. This differentiation implies that, even though they experienced the same exposure conditions, the respiratory responses of each organism were assessed independently. This approach allowed for the use of various individuals to replicate the experiment, providing independent data points.

(c) Statistical analysis

We quantified the metabolic scaling and its dependence on temperature and predation variation using linear models. As a first step, we developed *a priori* hypotheses about how temperature and predation variation should affect the metabolic scaling. First, we tested whether the slope was close to 0.75, as predicted by the MTE. Second, we tested whether the metabolic scaling slope was invariant, regardless of variation in temperature and predation pressure.

We used Bayesian likelihood in our study because it is flexible, accommodating the negative log-transformed values and allowing for accurate modelling through adaptable functions and prior distributions. Therefore, we translated these hypotheses into the following linear model:

$$\mathrm{logA} \sim \mathrm{Normal}\,(\mu, \sigma)$$

$$\mu = \alpha + \boldsymbol{\beta} X$$

where log metabolic rate (M) is normally distributed with an unknown mean μ and standard deviation σ; μ is defined by a linear model with an intercept α; and 10 fixed predictors are represented by $\boldsymbol{\beta} X$. These contain all main effects (body size, temperature levels and predation regime), where the model included all possible interactions for which we had *a priori* expectations. Predictor and response data represent single measurements of metabolic rate (n = 280 total observations). All variables were $\log_{10}$-transformed before model fitting. After transformation, predictor variables (including temperature) were centred to improve model fitting and interpretation.

We employed Bayesian inference to assess models, generating joint posterior distributions with No-U-Turn sampler using *rstan* via the *brms* [42] package in R. The main slope of body size was assigned a normal (0.75, 2) prior, corresponding to the 0.75 slope predicted by the MTE. Other priors were normal (0, 1), except for sigma, which was exponential (1). Despite being informed by previous work, these priors had minimal effect, as confirmed by a prior sensitivity analysis (electronic supplementary material, figure S1). We verified chain convergence with Gelman–Rubin statistics, ensuring all *Rhat* values were <1.1 [43], and assessed model fit using posterior predictive plots [44,45], summarizing results using joint posteriors.

3. Results

The mussel *B. pharaonis* showed important changes in the body-mass scaling of metabolic rate in response to both temperature and blue crab cue conditions. First, the metabolic scaling of the mussels both exposed and not exposed to crab cues showed a higher elevation (higher intercept) at the high versus low temperatures (from −0.13 to 0.23 and from −0.31 to 0.24, respectively; table 1). This implies that in both the presence and absence of crab predator

Table 1. Results of the linear regression analyses of $\log_{10}$ body size in relation to $\log_{10}$ metabolic rate of invasive mussels across temperature and crab predation regime.

predation cues	*n*	temperature	slope (95% CrI[a])	intercept (95% CrI[a])
no crab cues	52	13°C	0.43 (0.19–0.67)	−0.13 (−0.23 to −0.03)
	49	20°C	0.51 (0.37–0.76)	0.05 (0.00–0.11)
	53	27°C	0.60 (0.36–0.84)	0.23 (0.15–0.32)
crab cues	48	13°C	0.86 (0.63–1.07)	−0.31 (−0.40 to −0.22)
	53	20°C	0.69 (0.54–0.85)	−0.04 (−0.09 to 0.02)
	46	27°C	0.53 (0.27–0.79)	0.24 (0.15–0.33)

[a] CrI: Credible intervals represent the plausibility, based on posterior probability density, that parameter values fall within certain intervals.

cues, metabolic rate increased with increasing temperature. Second, for mussels that were not exposed to crab cues, we found no important differences in scaling slopes (0.43, 0.51 and 0.60, respectively) among the three experimental temperatures (figure 1 and table 1). Specifically, the probability was only 0.07% for a steeper response when the temperature increased from 13°C to 20°C, and it further decreased to 0.05% for the temperature range from 20°C to 27°C. Third, metabolic scaling relationships for mussels that were exposed to crab cues showed steeper slopes at 13°C and 20°C (0.86 and 0.69, respectively) than those seen in the absence of crab cues. However, at 27°C, the mussels showed a shallower slope resembling that seen in the absence of crab cues (0.53 versus 0.60, respectively) (figure 1 and table 1). Specifically, at 13°C, the metabolic scaling of the mussels exposed versus those not exposed to crab cues had a probability of 92.3% of being steeper. Similarly, at 20°C, the scaling slope of the mussels exposed versus those not exposed to crab cues has a probability of 38.9% of being steeper. While at 27°C, the probability of the slope being steeper was 0.05%, which is much lower than that observed at 13°C and 27°C. This implies that in the absence of crab cues, the metabolic rate increased with increasing temperature, irrespective of the mussels' size. However, in the presence of crab cues, the metabolic rate of the smaller mussels increased with increasing temperature, whereas that of the larger mussels stayed approximately the same.

4. Discussion

Our study highlights the important roles of temperature and predation risk in shaping mass-specific metabolic rates. Specifically, we observed an interactive effect of temperature and predator cues on the metabolic scaling of invasive mussels. To our knowledge, the study of predator–prey interactions and how they interact with temperature remains relatively understudied, especially in the context of invasive species, which remains entirely unexplored. As such, our study contributes novel insights into the complex interaction of intrinsic and extrinsic factors shaping metabolic responses.

Our research reveals notable deviations from the predictions of the MTE and provides support for the MLBH, highlighting the impact of temperature on variations in metabolic scaling. Moreover, we underscore that temperature is not the sole factor influencing metabolic scaling; other factors operate in conjunction with temperature to shape these patterns. Our study builds on previous studies showing the interactive effects of temperature and predator regime/cues on metabolic scaling in aquatic amphipods [26,27]. The metabolic scaling slope increased with temperature for amphipods from freshwater springs without fish predators but decreased with temperature for amphipods from springs with fish [27]. A similar reversal of the effect of temperature was observed for freshwater and estuarine amphipods in the absence versus the presence of chemical cues from fish predators [26].

Although interactive effects of temperature and predator cues were observed for the mussel *B. pharaonis*, these effects were not as pronounced as those observed in the above-mentioned amphipod studies. In particular, we found that there was no alteration in the metabolic scaling slope as temperature rose when crab predator cues were absent. Nevertheless, when crab predator cues were present, we observed a decline in the scaling slope as temperature increased, as observed in amphipods. At 27°C, the scaling slopes showed no change between treatments with and without crab cues, as revealed by overlapping 95% CIs (table 1). However, at 13°C and 20°C, strong interactive effects were observed where the metabolic scaling slopes were higher in the presence versus absence of crab cues. These differences occurred because at 13°C and 20°C the metabolic rate of small mussels decreased in the presence of crab cues, whereas that of larger mussels increased somewhat. However, such size-specific changes in metabolic rate were not observed at 27°C.

We hypothesize that these interactive effects are the result of the following two conflicting vital demands: avoiding predation versus avoiding suffocation. We assume that (i) small mussels with thinner shells are more vulnerable to crab predation than larger mussels with thicker shells [46–51] and (ii) opening shell valves facilitates respiratory ventilation and associated metabolic rate (as evidence, closed valves are associated with reduced metabolic rates in bivalve molluscs [52,53]). Accordingly, in colder conditions, smaller, vulnerable mussels close valves as an anti-predator measure, reducing metabolic rates compared to open valves without crab cues (figure 2). This aligns with an experimental study, indicating that blue crabs prefer small mussels, adjusting preferences based on shell strength versus profitability ratios [51]. Indeed, predator cues are known to induce closure of valves in mussels [54] and of opercula in barnacles [55]. Small mussels can afford to do this at low temperatures when their metabolic demands are relatively low. However, in high temperatures, small mussels prevent suffocation by

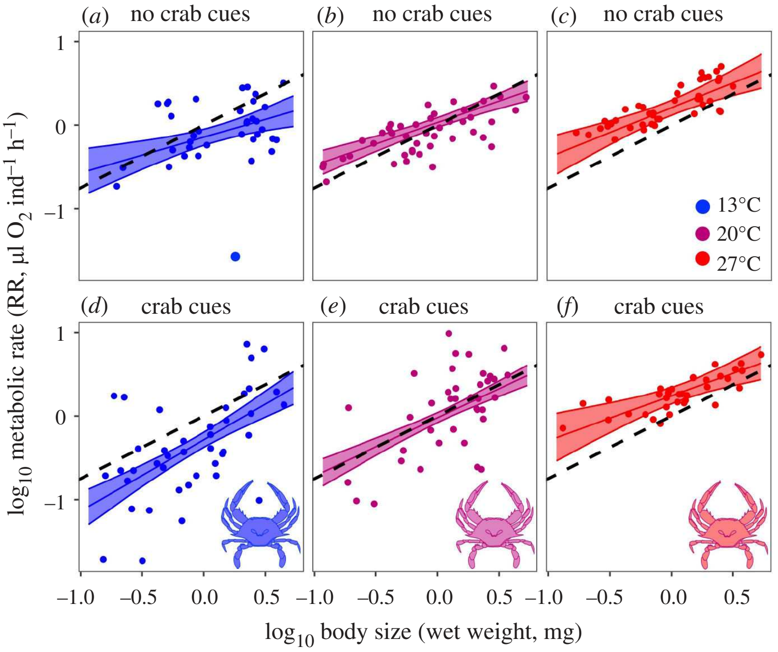

Figure 2. Relationships between metabolic rate and wet body mass of invasive mussel populations: (*a*) crab cues absent at 13°C, (*b*) crab cues absent at 20°C, (*c*) crab cues absent at 27°C, (*d*) crab cues present at 13°C, (*e*) crab cues present at 20°C and (*f*) crab cues present at 27°C. Black dashed lines indicate the expected 0.75 slope expected by MTE.

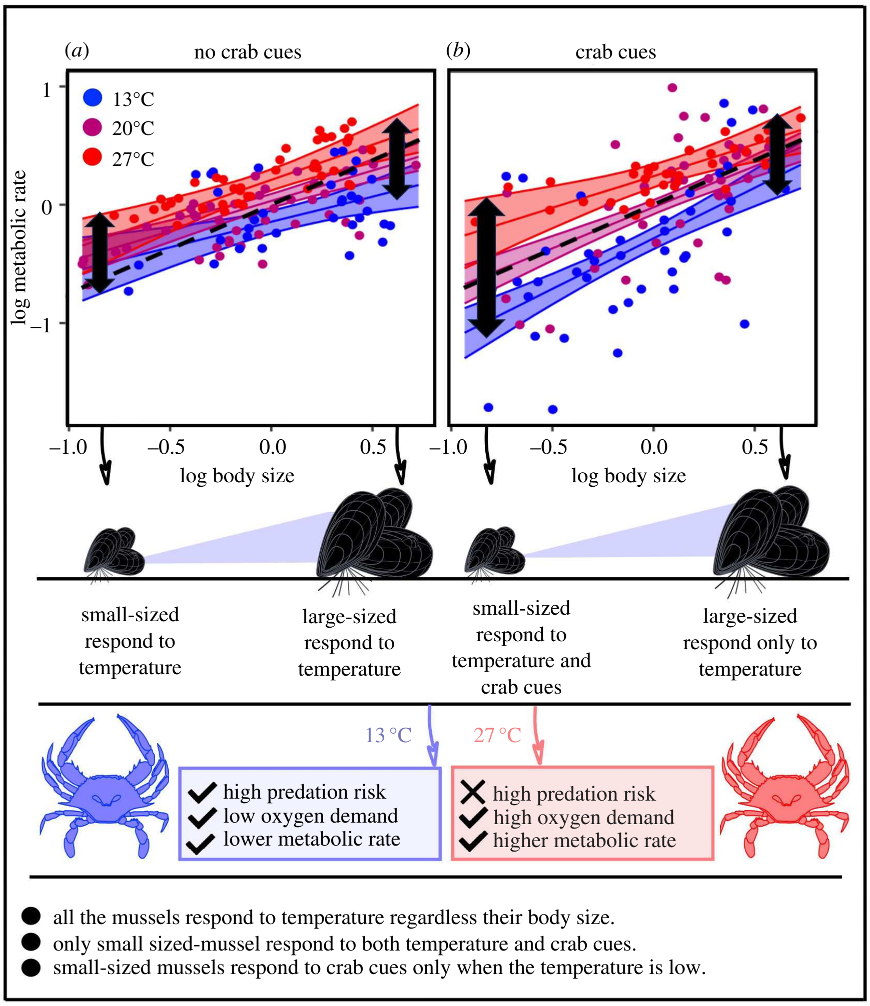

Figure 3. Schematic representation of some hypothetical causes of the differences in metabolic scaling observed among *B. pharaonis* populations: (*a*) without versus (*b*) with blue crab cues across temperature levels. The interactive effects probably arise from small mussels' dual needs to evade predation and oxygen demand to avoid suffocation. Their thinner shells make them more susceptible to crab predation, prompting valve closure to reduce metabolic rates as an anti-predator measure, particularly in colder temperatures. This aligns with blue crabs preferring small mussels, adjusting preferences based on shell strength. Therefore, while all mussels, regardless of size, increase their metabolism with increasing temperatures (e.g. by keeping their valves open to avoid suffocation), only small-sized mussels decrease their metabolism in response to crab cues and low temperatures (e.g. by closing their valves as an anti-predatory behaviour).

keeping their valves open, which elevates metabolism despite the presence of crab cues. This is because the demand for oxygen overrides their anti-predatory behaviour. This is also why, in the presence of crab cues, the small mussels only increase their metabolic rate at the highest temperature when the danger of suffocation is the greatest (figure 3).

By contrast, better-protected, large mussels, with thicker shells, do not need to close their valves in the presence of crab cues, thus retaining respiratory metabolic rates that are as high or higher than those seen in the absence of crab cues. Larger mussels can maintain open valves, regardless of crab cues, as temperatures rise, allowing them to increase metabolism under heat without responding to shifts in predation conditions (figure 3). This aligns with the significant energy costs they incur, mainly owing to the combination of high-temperature exposure, food intake and valve behaviour [56]. This behaviour underscores the remarkable ability of these organisms to adapt to their environment and optimize their energy usage in response to changing conditions.

5. Conclusion

Our findings demonstrate that the mass-dependent metabolic rate responses of invasive mussels to increasing temperatures are mediated by the presence or absence of blue crab predation cues. This highlights a complex interplay of temperature, predation and metabolic responses in shaping the behavioural and metabolic physiology of invasive species. Our study is a stepping stone towards better understanding the complex interactions among predation-induced behaviours, temperature-driven physiological demands and metabolic responses of invasive species. Documented interactive effects on metabolic rate primarily involve body size, temperature or both [57]. To better comprehend variations in metabolic rate, beyond size and temperature, we should explore additional concurrent factors. This holistic approach is vital when studying the realistic ecological impacts of global warming.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. All data, R code and electronic supplementary material used for the analyses are available online from the Dryad Digital Repository [58].

Electronic supplementary material is available online at [59].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. V.G.: conceptualization, data curation, formal analysis, investigation, methodology, supervision, visualization, writing—original draft, writing—review and editing; G.M.: conceptualization, methodology, writing—review and editing; D.S.G.: conceptualization, methodology, writing—review and editing; J.S.W.: formal analysis, funding acquisition, writing—review and editing; M.B.-B.: data curation, methodology, writing—review and editing; F.P.M.: data curation, methodology, writing—review and editing; M.F.T.: data curation, methodology, writing—review and editing; M.N.: data curation, methodology, writing—review and editing; G.S.: supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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