

## Research



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# Coral reef fishes reveal strong divergence in the prevalence of traits along the global diversity gradient

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Coral reefs are experiencing declines due to climate change and local human impacts. While at a local scale these impacts induce biodiversity loss and shifts in community structure, previous biogeographical analyses recorded consistent taxonomic structure of fish communities across global coral reefs. This suggests that regional communities represent a random subset of the global species and traits pool, whatever their species richness. Using distributional data on 3586 fish species and latest advances in species distribution models, we show marked gradients in the prevalence of size classes and diet categories across the biodiversity gradient. This divergence in trait structure is best explained by reef isolation during past unfavourable climatic conditions, with large and piscivore fishes better represented in isolated areas. These results suggest the risk of a global community re-organization if the ongoing climate-induced reef fragmentation is not halted.

## 1. Background

Coral reefs are the most diverse marine ecosystems and show steep biodiversity gradients in numerous taxa that support a multitude of ecological functions and ecosystem services [1–5]. Concern has globally emerged about the future of this system as reefs are threatened by the combination of habitat loss and degradation due to climate change and local human impact such as overfishing [6–8]. Coral reef biodiversity is expected to be increasingly exposed to these effects. Coral bleaching may become an annual phenomenon for most coral reefs in less than 20 years [9], and fishing pressure is increasing with little capacity to move towards more sustainable practices [10]. In this context, identifying the mechanisms associated with community assembly and disassembly across the species richness (SR) gradient is important to elucidate potential effects of biodiversity erosion on this system.

On coral reefs, analysis of the previous literature suggests a closer examination of the role of the eco-evolutionary processes that determine community structure. While it is widely documented that biodiversity loss may produce severe shifts in the taxonomic and trait structure of communities at local

scale [11–14], biogeographical analyses suggested a remarkably consistent taxonomic structure across the globe for both corals and fish [15,16]. This would mean that despite strong evolutionary [17–19], environmental [2,4,20], geographic [5,21] and geological drivers [22,23], the relative importance of families at regional scale generally would not deviate much from a random subset of the global species pool [15]. However, biogeographical patterns expressed solely in taxonomic terms may not capture the breadth and distribution of species' traits that are potentially correlated with ecosystem functioning [24]. Body size, for instance, is associated with a number of fish ecological characteristics such as growth, mortality and trophic level. Moreover, colonization capacity, defined here as the capacity of species to reach isolated locations from larval dispersal or as active adult migration, may limit the distribution of species in isolated locations [25,26]. At the same time, diet may also determine the distribution of species according to resource availability and evolutionary mechanisms [27,28].

In this study, we examine the prevalence of two important species traits for tropical reef fishes, namely body size and diet [28], across the global biodiversity gradient. Then, we use statistical modelling to evaluate whether contemporary or historical factors best explain observed patterns. We hypothesize that the trait structure of reef fish assemblages significantly varies across the biodiversity gradient. Specifically, the prevalence of body size classes in regional assemblages of tropical reef fishes would be primarily explained by the isolation from Quaternary refugia, as already shown for SR [29] with a greater proportion of large-bodied species in the most isolated reef areas. Then, the prevalence of certain diet categories would be more strongly influenced by the area of tropical reefs, which can reflect the level of resources availability [30].

## 2. Material and methods

### (a) Distributional and trait data on reef fishes

We used a global database on tropical coastal fish occurrences previously compiled [31]. These data consist of the global distribution of 6316 fish species defined according to a grid of  $5^\circ \times 5^\circ$  resolution, corresponding to approximately  $550 \times 550$  km at the equator. Out of these species, we used distributional data for the 3586 species considered in the fish phylogeny.

We focused our analysis upon two major species ecological traits: maximum body size and diet.

In fishes, body size is related to a number of ecological characteristics that impact species fitness such as fecundity [32], metabolism [33], dispersal [34], growth and mortality rates [35]. Similarly, fish diet influences species metabolic rate [36], growth rate [37], and rates of food ingestion and nutrient excretion [38], and is associated with past diversification rates [28].

Maximum body size in centimetres was extracted from FishBase while species diet was described according to eight trophic guilds defined according to quantitative analysis of fish gut content data and reef fish phylogeny [39]. This analysis uses detailed gut content information for 615 reef fish species and their phylogenetic position to assign species to the following trophic guilds: herbivores, microvores and detritivores (HMD), planktivores, sessile invertivores, corallivores, microinvertivores, macroinvertivores, crustaceivores, and piscivores (see [39] for an extensive description).

### (b) Statistical analysis

In order to test whether the taxonomic and trait structure of reef fish assemblages was stable along with the global biodiversity gradient, we performed three multinomial Bayesian models that predict the probability for a species to belong to a family or a certain trait category (either a body size class or a trophic guild) according to the local SR. For this analysis, similarly to Mouillot *et al.* [16], we defined body size according to six categories: 0–7 cm, 7.1–15 cm, 15.1–30 cm, 30.1–50 cm, 50.1–80 cm and greater than 80 cm. We decided to treat size as a categorical variable for consistency with the analysis of the relative importance of fish families and trophic guilds.

Bayesian models were performed using the *brms* package in R using a multinomial logit link function. The probability for a species to belong to a certain family or trait (either size category or trophic guild) is computed as follows:

$$\Pr(k|\mu_1, \mu_2, \dots, \mu_k) = \frac{\mu_k}{\sum_1^k \exp(\mu_i)}, \quad (2.1)$$

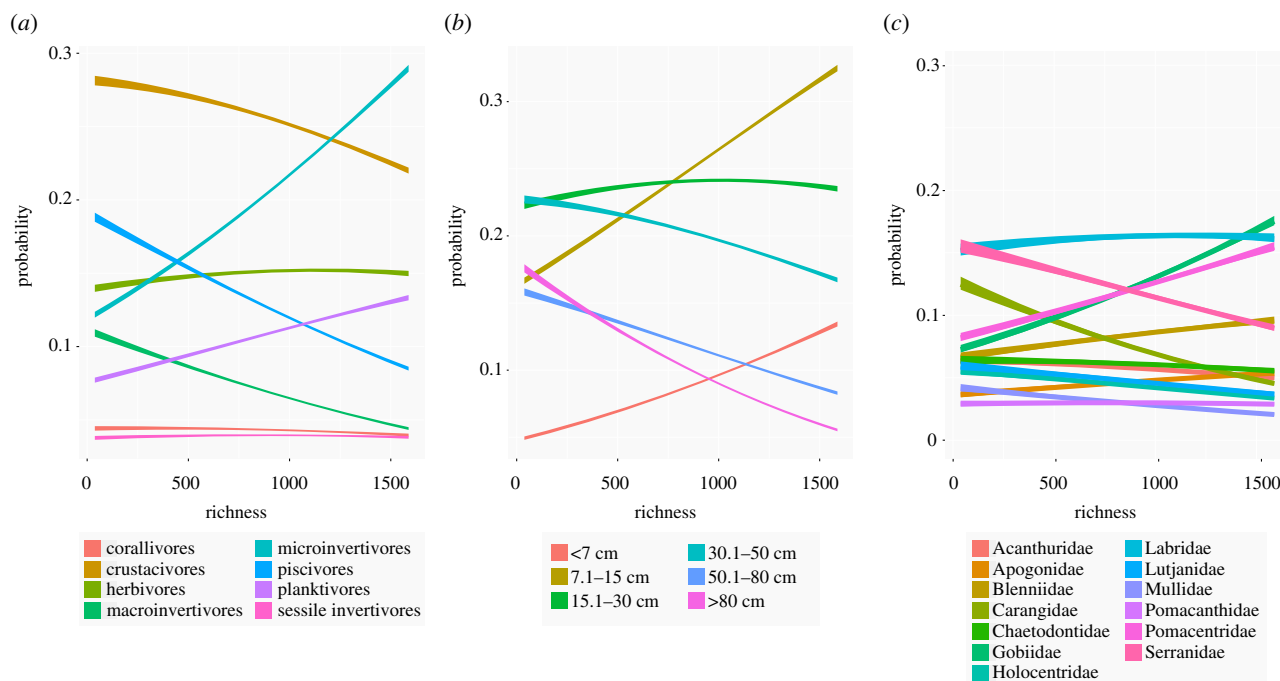
with  $\mu_k$  defined as

$$\mu_1 = 0, \mu_{k|2:n} = \beta_{0k} + \beta_{1k} \ln(\text{SR}), \quad (2.2)$$

where  $\beta_{0k}$  is the intercept of the family-specific or category-specific fixed effect,  $\beta_{1k}$  is the slope for the natural log-transformed SR for each family or category  $k$  (either body size classes or trophic guilds) and  $n$  is the number of families or categories (six in the case of body size classes and eight in the case of trophic guilds). For both body size and trophic guilds models, we used uninformative priors and ran the model for four chains using 5000 iterations per chain after 1000 warm-up iterations.

We then tested whether species body size and diet play a role in determining the spatial distribution of species. In other words, we tested whether the presence–absence of a species in a given location is due to the environmental characteristic of the location, the ecological characteristic of the species or the interaction between environment and the species traits. Understanding whether the environmental response of species is due to their ecological characteristics is known as the fourth-corner problem, that is the study of the environment–trait association using matrices of the presence–absence across species, environmental data across locations and trait data across species. The matrix of environment–trait interaction coefficients is the fourth corner [40]. We used the generalized joint attribute modelling (GJAM) approach proposed by Clark *et al.* [41], which solves the fourth-corner problem accounting for the joint distribution of multiple species, thereby accounting for their potential interaction. In particular, the GJAM approach was used to model the presence–absence of the 3586 species in each grid cell according to sea surface temperature, present coral reef area, present geographical isolation from coral reefs, coral reef area during the Quaternary and geographical isolation from coral reefs during the Quaternary. These variables were selected because they have already been shown as important correlated of SR [4,29]. Mean SST ( $^\circ\text{C}$ ) for each grid cell was obtained from the Bio-ORACLE database at a resolution of 5 arcmin [42]. Estimates of coral reef area ( $\text{km}^2$ ) were obtained from data based on the Coral Reef Millennium Census project and available at <http://data.unep-wcmc.org/>. Isolation estimates were calculated using the nearest neighbour approach. Isolations from present reefs, from reefs during the Quaternary and coral reef area during the Quaternary were obtained from Pellissier *et al.* [29].

For this analysis, trophic guilds were treated as categorical variables, thus producing one slope for each guild–environmental variable combination, while maximum body size was treated as a continuous variable in order to reduce the risk of potential biases related to the categorization of this variable. Positive slope coefficients for the interaction between



**Figure 1.** Marginal effects of SR on the probability for a fish species to belong to different (a) trophic guilds (diet), (b) body size classes or (c) families. (Online version in colour.)

environmental variables and trophic guilds indicate that a certain environmental variable favours the presence of species that belong to a particular guild, while negative values indicate that a certain environmental variable favour the absence of species that belong to a particular guild. Instead, for maximum body size, positive slope coefficients for the interaction between body size and environmental variables indicate that that particular environmental variable favours the presence of large species and negative values indicate that the environmental variable favour the presence of smaller species.

### 3. Results and discussion

In general, our results are largely consistent with the already documented stability in the relative contribution of fish families to SR (figure 1). Some families with largely consistent traits varied across the global biodiversity gradient. For example, the proportion of Gobiidae and Pomacentridae increased with SR, while Serranidae and Carangidae decreased. However, in agreement with previous research, the relative importance of most families remained relatively stable along with the global gradient in SR [15].

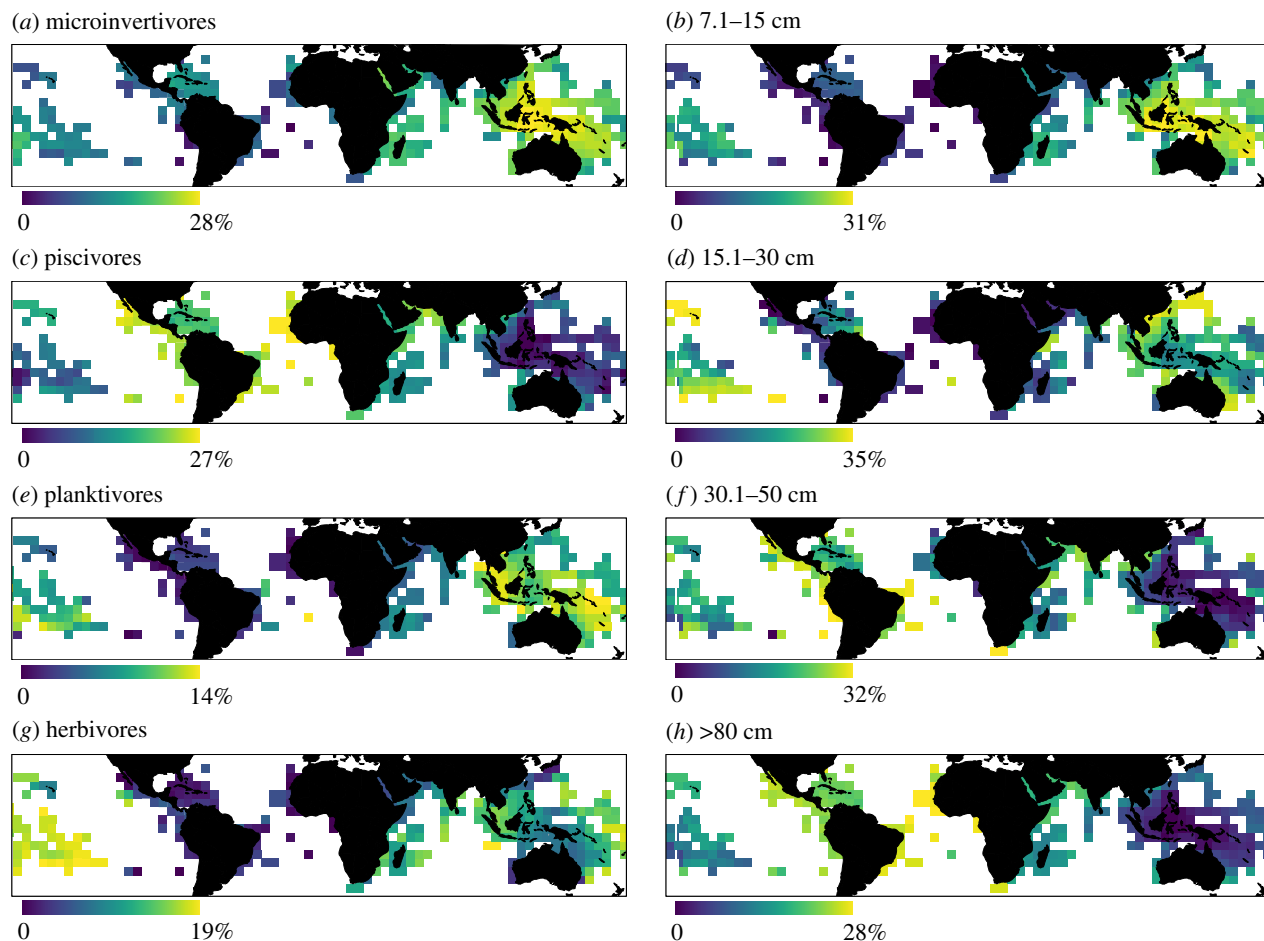
Nevertheless, the dominance of ecological traits markedly differs among reef fish assemblages at the global scale (figure 1). For instance, piscivores represent up to 20% of the SR in the Tropical Eastern Pacific, while they do not exceed 12% in the Indo-Pacific—the richest areas of the Indo-Australian Archipelago (figure 2). Similarly, large species (greater than 80 cm in body size) constitute up to 40% of the total SR in the Eastern Atlantic but only 6% in the Indo-West Pacific.

Small species tend to dominate species-rich areas in both the Indo-Pacific and the Atlantic, while larger species are proportionally dominant in more depauperate reefs. A similar pattern can be identified for diet categories. Microinverteviores and planktivores tend to dominate in the richest areas while poorer reefs appear to be dominated by piscivores, macroinverteviores and crustacivores.

In order to test whether regional assemblages can be considered a random subset of the global species pool, we built two Bayesian multinomial models that quantify the probability of a species to belong to the different trait categories for both diet and maximum body size. Species body size was defined according to six categories as in Mouillot *et al.* [16], while the diet was described according to the eight categories recently proposed by Parravicini *et al.* [39] on the basis of assembled gut content data.

Our results highlight a remarkable divergence in the relative importance of traits across the SR gradient for both maximum body size and species diet (figure 2). With the exception of few trait categories (i.e. sessile inverteviores, corallivores and species of intermediate body size from 15 to 30 cm), all the other trait categories displayed an uneven probability of occurrence across the global gradient of SR. In poorer assemblages, a species has a higher probability of being large-bodied (greater than 30 cm) and either crustacivore or piscivore. On the other hand, in highly diverse locations, a species has the highest probability of being small-bodied (less than 15 cm) and having a microinverteviores diet.

The relatively stronger variation we found for traits compared to fish families suggests that species may respond more to ecological traits than taxonomy itself, especially in the case of families that show a large range of traits (e.g. Labridae) (figure 2). Therefore, in order to further explore the role of traits in determining the composition of regional assemblages, we used species-level models. We hypothesized that the same drivers of SR may have interacted with certain traits across evolutionary time scale, thereby producing assemblages with markedly different trait structures. In order to test for such interaction, we took advantage of the latest advances in species distribution modelling. Specifically, we used the same correlates of reef fish SR (sea surface temperature, present reef area, past reef area, present geographical isolation and past geographical isolation) as in Pellissier *et al.* [29], and we built joint species distribution models



**Figure 2.** Global gradients in the proportion of fish species belonging to different trophic guilds and body size classes. (Online version in colour.)

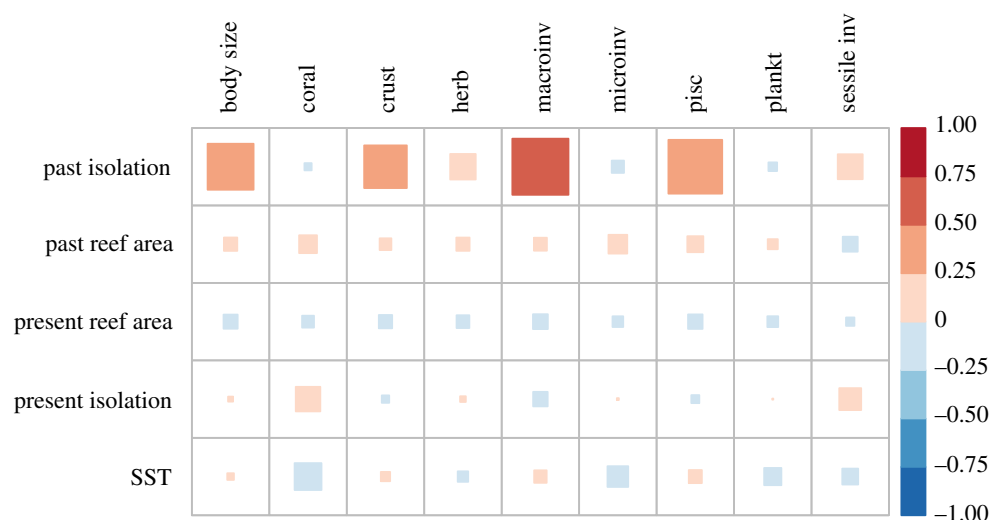
using the GJAM modelling approach developed by Clark *et al.* [41]. We used such a technique to model the joint distribution of all the species according to present and past environmental variables, their ecological traits and the interaction between environmental variables and ecological traits. For this particular analysis, body size was considered as a continuous variable; while species diet was described with the above mentioned eight categories.

The technique allowed us to identify a major role of ecological traits in determining species distribution (figure 3). In particular, both body size and diet strongly interacted with the isolation of coral reefs from refugia during the Quaternary. Indeed, our results suggest that past isolation caused by the Quaternary glaciations may have particularly favoured large species, and among them, piscivores, crustaceans and microinvertivores.

Overall, our results suggest that past environmental changes left a strong imprint on the trait structure of regional assemblages of reef fishes, and more particularly the isolation of reefs during unfavourable climatic events. During the Quaternary period, which was accounted for in our model, repeated periods of global cooling and warming caused coral reef to contract and expand [28]. Older isolation processes, not explicitly considered in our study, may also explain the observed prevalence of ecological traits globally. The historical biogeography of reef fishes [43] suggests that from the Oligocene onward, the Indo-Pacific experienced a history of connectivity, while the Eastern Pacific and the Atlantic were subjected to a history of isolation. The connectivity of the Indo-Pacific culminates during the Pliocene. In this favourable period, coral reefs were expanding [17], and species originated

in the IAA with subsequent movement toward the Central Pacific and the Indian Ocean. By contrast, during this period, the Tropical Eastern Pacific and the Atlantic Oceans were experiencing a contraction of their species pool probably due to extinction and increased isolation of their coral reefs [18]. In this context, our results support the hypothesis that large carnivores, with high colonization capacities and post-dispersal persistence abilities [25,44] had greater chances of survival or recolonization in the Atlantic and Tropical Eastern Pacific than smaller species. This process holds within oceanic realms with large carnivores characterizing depauperate locations that experienced extreme isolation in the past, or that are isolated from rich reef areas by barriers [43] or geographic distance [2,4,5]. Large species may therefore have been favoured in species-poor locations, presumably because of their ability to persist when facing unfavourable conditions or to better colonize after regional extinctions. By contrast, small species appear to have persisted better in locations with a high coral reef area, such as the IAA and the Caribbean. These biodiversity hotspots with large and less fragmented coral reefs have possibly favoured the diversification (or at least the persistence, i.e. less extinctions) of small-bodied fish species (mostly microinvertivores) that have comparatively higher population turnover rates, speciation rates [45] and therefore greater contribution to richness in these assemblages.

Dispersal appears as an important mechanism underlying the distribution of traits in reef fish assemblages [46]. However, while dispersal abilities influence the colonization capacity of species, their persistence also depends on their ability to exploit local resources and the traits selected by evolutionary history [28,47,48].



**Figure 3.** Slope coefficients returned by the generalized joint attribute model and referred to the interaction between species traits and environmental variables. Positive values correspond to a positive effect of the interaction in determining the presence of species while negative values indicate a negative effect on species presence. Body size is a continuous variable while diet is described according to eight trophic guilds (coral: corallivores, crust: crustaceans, herb: herbivores, macroinv: macroinvertebrate feeders, microinv: microinvertebrate feeders, pisc: piscivores, plankt: planktivores, sessile inv: sessile invertebrate feeders). (Online version in colour.)

The high contribution of planktivores to SR in the IAA is suggested to have been driven by extinctions outside this region during the Quaternary [49]. High diversification rates of corallivorous and herbivorous trophic guilds in the IAA during the Miocene (past 20 Myr) also adds to the current trait pattern [43]. At the ecological scale, resource use (and abundance) could have shaped the distribution of trophic guilds, such as piscivores on small and isolated reefs [50] and planktivorous species partitioning and feeding on abundant and constant plankton supplies in the IAA [49].

The spatial patterns reported here are inherently dependent on the coarse definition of traits that is presently available at a global scale. A better understanding of mechanisms will benefit from higher-resolution data in the future, but that is presently unavailable at the global scale. Although based on coarse categorization of species, our results still highlight two aspects of major concern when considering the present threats to coral reefs. First, we detected a variable trait structure of fish assemblages across the global biodiversity gradient, which suggests the potential for a re-organization of the structure of communities in the case of regional species loss. Second, our findings suggest that the trait structure of reef fish assemblages at the regional scale reflects the interaction between species' colonization capacity with reef isolation across unfavourable climatic periods. Future projections predict that the increasing frequency of coral bleaching may increase the fragmentation of reefs, which already showed a significant effect on the population dynamics of corals [51]. While the effect of coral bleaching cannot be paralleled to that of Quaternary climatic oscillations, large-scale mortality events may isolate certain reefs, altering the unique trait structure of reefs that benefit from high connectivity, such as those from the global biodiversity hotspot.

We cannot address the vulnerability of assemblages inherited from the past. However, our results suggest that

sustaining connectivity may be key in preventing changes in community structure potentially triggered by the loss of species with limited colonization ability. While our patterns focus on broad traits such as body size and diet, future studies are needed to improve our understanding of fish traits and their links with ecosystem functioning, and to inform local management.

**Data accessibility.** The data are provided in the electronic supplementary material [52].

**Authors' contributions.** V.P.: conceptualization, data curation, formal analysis, methodology and writing-original draft; M.G.B.: conceptualization, data curation, methodology and writing-original draft; S.V.: conceptualization, formal analysis, methodology, writing-review and editing; F.L.: conceptualization, methodology, writing-review and editing; F.G.A.D.: data curation, writing-review and editing; L.P.: methodology, writing-review and editing; S.R.F.: conceptualization, methodology, writing-review and editing; E.L.R.: conceptualization, methodology, writing-review and editing; D.M.: conceptualization, writing-review and editing; M.K.: conceptualization, data curation, funding acquisition, methodology, project administration, writing-review and editing.

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

**Competing interests.** We declare we have no competing interests.

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