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Testing differences in thermal tolerance between two amphibians with contrasting invasion abilities

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Physiological traits may influence the establishment success of non-native species, yet empirical links between physiology and invasiveness remain limited. The American bullfrog (*L. catesbeianus*) and the green frog (*L. clamitans*) are closely related species with overlapping native ranges in the eastern United States, but have contrasting invasion histories: bullfrogs have colonized much of the western U.S., while green frogs have not. One hypothesis that could explain this pattern is that invasive species possess greater tolerance to heat stress and enhanced capacity for thermal acclimation. To test this hypothesis, we compared critical thermal maximum (CT_{MAX}) and acclimation capacity in tadpoles of both species from within their native range. We found that the species both exhibit equally high CT_{MAX}. Further, neither species was able to acclimate to a warmer temperature. However, while bullfrogs showed no change in CT_{MAX} after acclimation, green frogs experienced a slight reduction in CT_{MAX}, suggesting that they may be more sensitive to warming than bullfrogs. These results suggest that intrinsic differences in thermal tolerance and plasticity alone do not explain bullfrog invasion success. Other factors—such as competitive dominance, rapid evolutionary shifts, or interacting abiotic and biotic pressures—may facilitate bullfrog persistence in novel, warmer habitats of the western U.S.

KEYWORDS

acclimation capacity, bullfrog, critical thermal maximum, green frog, invasive species, tadpole

Introduction

Invasive species are a leading cause of global biodiversity loss (McKinney and Lockwood, 1999; Mooney and Cleland, 2001). Yet, the proportion of introduced species that become established invasives in new environments is relatively low (Williamson, 1996). Uncovering which traits promote invasiveness can provide insights into why some species become invasive whereas others do not (DeVore et al., 2021). Many ecologically

important traits are likely to facilitate invasion, for example, fast life histories that include rapid growth rates and high fecundity (Sakai et al., 2001). More recently, there has been considerable interest in understanding whether greater physiological tolerance to stress promotes invasions (Jarnevich et al., 2018). However, few empirical studies investigate the relationship between invasion success and key physiological traits that play a role in the establishment of non-native species in a new habitat (Kelley, 2014).

In general, the physiological traits associated with invasiveness could permit species to occupy new environments that differ from their native ones, and they may have greater tolerance to stressors such as temperature, desiccation, and disturbance (Olyarnik et al., 2009). For ectotherms, temperature is a particularly important factor influencing the geographic distribution of a species (Bozinovic et al., 2011). Key physiological traits may therefore include broad thermal tolerances that allow a species to exist within a wide thermal range and especially to tolerate high temperatures (Zerebecki and Sorte, 2011), and increased thermal plasticity (acclimation capacity) that allows an organism to recalibrate its thermal threshold after brief exposure to different environmental temperatures (Buckley et al., 2001; Mittan and Zamudio, 2019) enabling function over a wider range of temperatures. Indeed, aquatic ectotherms such as tadpoles may be constantly challenged by high temperatures because their small body size coupled with the high heat capacity of water results in body temperatures that are equal to that of the water (Duarte et al., 2012). However, species with the propensity to become invasive may produce tadpoles with intrinsically higher heat tolerances and acclimation capacities than others.

A powerful approach to testing associations between physiological traits and invasiveness is to compare these traits in closely related species where one is a successful invader and the other is not. The American bullfrog, *Lithobates catesbeianus*, and the green frog, *L. clamitans*, are congeners that largely occupy the same native range in the eastern United States (Harding and Mifsud, 2017; Figures 1A, B). Bullfrogs are considered one of the 100 worst invasive species globally (Lowe et al., 2000) and have successfully expanded into new habitats in the western and southwestern United States, among 40 other countries across four continents (Lever, 2003). They were likely introduced in western North America between 1882 and 1904 (Jennings and Hayes, 1985) and have since established vigorous populations in much of the western U.S. (Figure 1 (IUCN, 2020)). Some of the places that bullfrogs have become established include areas such as California's Central Valley and parts of New Mexico and southern Utah in which maximum temperatures are much greater than those in the native range of the two species (Figure 1; Fick and Hijmans, 2017). By contrast, established green frog populations are only documented from a handful of localities outside their native range where they were introduced, including Newfoundland and British Columbia, Canada, and northern Utah and Washington, U.S. (Figure 1 (IUCN, 2020)). Although the ecological impacts of these few green frog introductions remain largely unknown, populations in Utah and Washington have been documented since 1966 (Gregoire and Powell, 2023), but have yet to expand in the same capacity as bullfrogs suggesting that green frogs lack traits that

promote invasiveness. Previous studies exploring the causes of variation in invasiveness between the two species have focused on differences in their diet (Werner et al., 1995), gut microbiota (Fontaine and Kohl, 2020), susceptibility to toxins (Birdsall et al., 1986) and community interactions (Hecnar and M'Closkey, 1997), but to our knowledge, there is no information on intrinsic thermal physiological differences of the tadpoles of the two species. This is particularly important, as tadpoles are a critical life stage, and potentially more vulnerable to physiological stressors such as temperature due to their small body size and the high thermal conductance of water (Lutterschmidt and Hutchison, 1997; Winter et al., 2016).

Bullfrogs and green frogs therefore present an opportunity to test predictions about the relationship between physiological traits and invasive ability. Here, we compared physiological traits in bullfrog and green frog tadpoles occurring in a northern part of their native habitat in the eastern U.S. We hypothesized that the critical thermal maximum (CT_{MAX}), i.e., the temperature at which locomotor function ceases (Lutterschmidt and Hutchison, 1997), and capacity to acclimate to higher temperature should differ between bullfrog and green frog tadpoles within their native range. In particular, we predicted that bullfrog tadpoles should have intrinsically higher CT_{MAX} , and a greater capacity to acclimate to higher temperatures. We tested these predictions using wild-caught tadpoles originating from a large semi-natural pond complex in southwestern Michigan.

Materials and methods

Tadpole collection and lab acclimation

In May and June 2022, we collected 77 wild bullfrog and green frog tadpoles ($n = 42$ bullfrogs and $n = 35$ green frogs) from the W.K. Kellogg Biological Station Experimental Pond Lab at Michigan State University. This research facility houses 18 experimental ponds that are currently colonized by natural flora and fauna including thriving populations of bullfrogs and green frogs. A logger was placed in one of the ponds to measure the natural temperature regime and inform acclimation temperatures during experiments (Supplementary Figure S1). Using long dip-nets, we collected tadpoles between Gosner stages 25–38 (Gosner, 1960) i.e., individuals in the 'tadpole' developmental stage prior to metamorphosis (McDiarmid and Altig, 1999). We then placed two conspecific tadpoles of similar size in rectangular plastic containers (31 x 17 x 9 cm) filled with filtered pond water. Containers were placed within temperature-controlled incubators (Percival Scientific, model I36LLVL) that were held for 2 days at 14°C (for 16 hours) in the day and 10°C (for 8 hours) at night and subjected to a light-dark cycle of 16:8 h L:D, typical of summer months in Michigan.

Critical thermal maxima

To compare heat stress tolerance, we measured the critical thermal maximum (CT_{MAX}), i.e., the temperature at which an organism begins to lose locomotor function (Lutterschmidt and Hutchison, 1997) in 17 bullfrog and 15 green frog tadpoles.

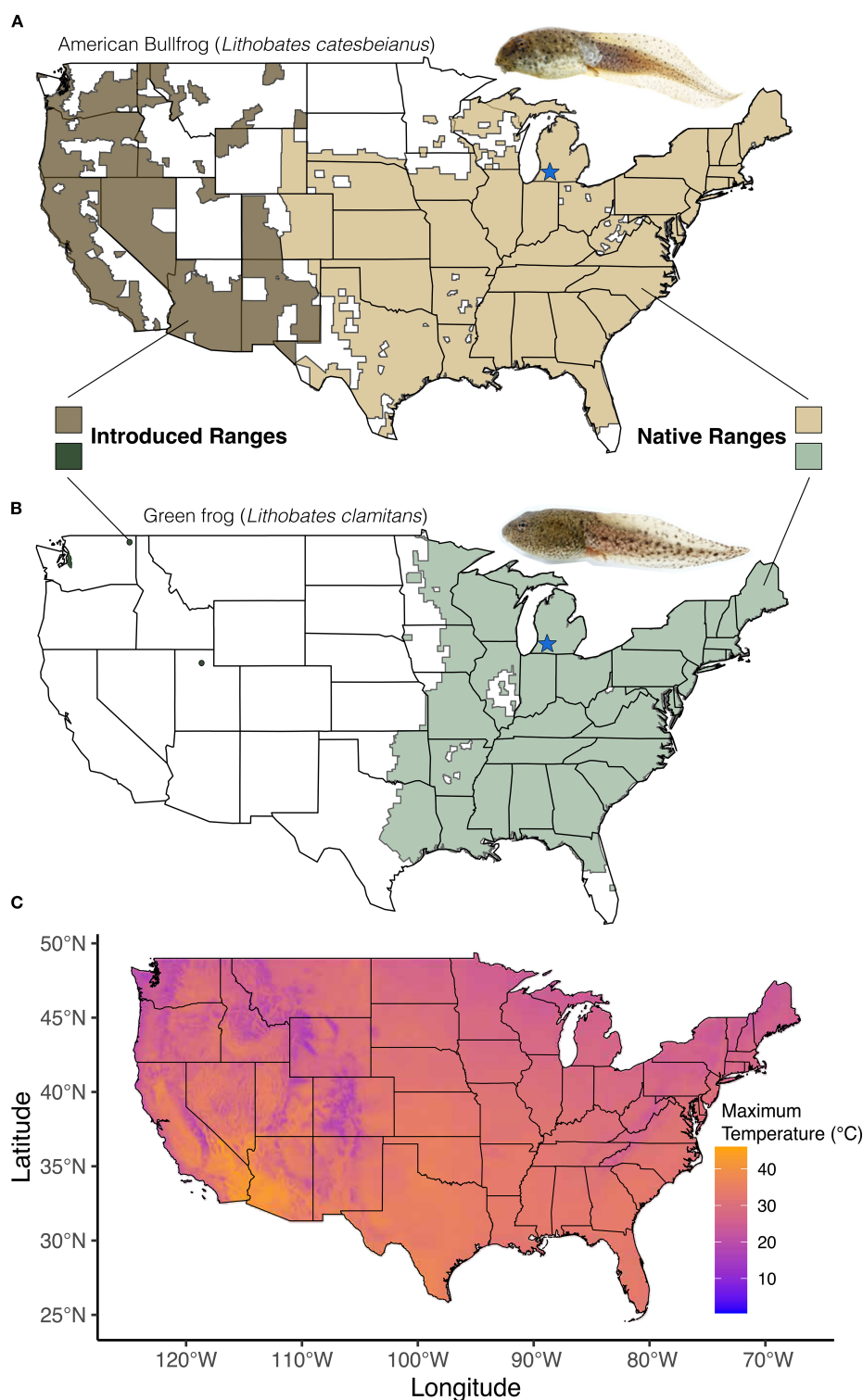


FIGURE 1

Species range map of bullfrogs and green frogs in the United States. **(A)** bullfrog native (light brown) and introduced (dark brown) US range. Sampling locality indicated by blue star. **(B)** green frog native (light green) and introduced (dark green) U.S. range. Sampling locality indicated by blue star. Range data for both species were used from IUCN database, 2022. **(C)** Maximum temperatures across the U.S. – from 1970–2000 (data from WorldClim 2).

Tadpoles were placed in individual mesh containers, partially submerged in a water bath filled with filtered pond water and held at 14°C. The mesh containers confined the tadpoles but

allowed them to experience the surrounding water. We then increased the water temperature by 0.3°C per minute, a standard rate for CT_{MAX} experiments in aquatic animals (Dallas and Rivers-

Moore, 2012; Gutiérrez-Pesquera et al., 2016) using a custom-built programmable temperature controller connected to a 500 W aquarium-grade titanium heating rod. A water pump was used to ensure homogenization of temperature in the water bath. Approximately every 1–2 minutes, we assessed tadpoles by turning them over onto their backs and watching their response. We defined CT_{MAX} as the temperature at which tadpoles failed to right themselves when turned over (Lutterschmidt and Hutchison, 1997). When tadpoles reached this point, they were rapidly removed from the experimental bath and placed in cool (14°C) pond water to recover. All tadpoles recovered, i.e., resumed normal swimming activity. Following the experiment, we measured the wet mass of each tadpole.

Thermal acclimation capacity

We measured thermal acclimation, which represents reversible plasticity in heat tolerance and can develop over days-to-weeks of sustained exposure to altered environmental temperatures (e.g., Cupp, 1980; Lapwong et al., 2021; Rohr et al., 2018). We placed newly caught tadpoles (15 bullfrogs and 10 green frogs) in an incubator set to reach a maximum of 20°C (for 16 hours per day), and a minimum nighttime temperature of 16°C (held for 8 hours per day) for 6 days. This acclimation temperature was higher than the baseline experiment, but still well within the natural range of variation in the pond temperatures (see Supplementary Figure S1). We chose an acclimation period of 6 days because this period is thought to be long enough to allow physiological changes to take place during thermal acclimation in amphibians (Brattstrom, 1968; Hutchison, 1961). Then, following the same protocol as above, we measured CT_{MAX} .

Statistics

All statistical analyses were performed in R Studio v 2024.04.2 (Posit Team, 2024). To test the prediction that bullfrog tadpoles are more tolerant of heat stress than green frog tadpoles, we performed a linear regression analysis to investigate how CT_{MAX} varies between the two species, while controlling for mass. Mass and Gosner stage were strongly correlated, ($r(28) = 0.4$, $p = 0.03$), and Gosner stage had no effect on CT_{MAX} ($t = -0.60$, $p = 0.56$). We, therefore, did not include Gosner stage in the analysis. Two data points were dropped from the analysis because the tadpoles did not look healthy at the start of the experiments. Next, to assess acclimation capacity, we conducted a linear regression analysis to examine the effects of acclimation temperature (i.e., 14°C or 20°C) on CT_{MAX} of the two species. Our model evaluated the main effects of acclimation temperature and the interaction between species and acclimation temperature on the response variable, CT_{MAX} , while controlling for mass.

To provide an estimate of acclimation capacity, an acclimation response ratio (ARR, Claussen, 1977) was calculated for each species, using:

$$ARR = \frac{\Delta CT_{MAX}}{\Delta Temperature}$$

where, ARR is the acclimation response ratio, ΔCT_{MAX} is the difference between CT_{MAX} after acclimation to the high temperature and CT_{MAX} after acclimation to the low temperature; and $\Delta Temperature$ is the difference between high and the low acclimation temperatures. Higher ARR values indicate greater acclimation capacity. After all experimentation, we euthanized tadpoles by applying a $\sim 1/8^{\text{th}}$ teaspoon of 20% benzocaine cream to their ventral sides until no movement or breathing was detected. All tadpoles were stored in 70% ethanol and assigned a Gosner stage.

Results

Critical thermal maxima

We found no significant difference in CT_{MAX} between the two species ($F_{(1, 27)} = 3.82$, $p = 0.06$). Qualitatively, however, green frogs appeared to have lower CT_{MAX} than bullfrogs. Mean CT_{MAX} values were 38.2°C for bullfrogs and 37.5°C for green frogs (Figure 2). The effect of wet mass on CT_{MAX} was also non-significant ($F_{(1, 27)} = 2.52$; $p = 0.12$).

Thermal acclimation capacity

Our results indicated that the species do not differ in acclimation capacity, i.e., there was no significant interaction between acclimation temperature and species (Figure 2; $F_{(1, 50)} = 0.46$; $p = 0.50$). However, after acclimation to the warmer temperature, green frogs had significantly lower CT_{MAX} than bullfrogs ($F_{(1, 50)} = 11.62$; $p < 0.01$). Mean CT_{MAX} values did not change for bullfrog tadpoles (CT_{MAX} after warm acclimation = 38.2; ARR = 0) but decreased for green frog tadpoles (CT_{MAX} after warm acclimation = 37.2; ARR = -0.03).

Discussion

Researchers are increasingly recognizing that physiological traits, such as tolerance to environmental stress, may predispose some species to invading and colonizing new habitats. Although bullfrogs and green frogs have been frequently studied within an invasive-native species context (e.g., Fontaine and Kohl, 2020), to our knowledge, there is no information on intrinsic thermal physiological differences in the juveniles of the two species.

When subjected to ramping heat-stress experiments after a brief acclimation to a cool, average springtime pond temperature (14°C), bullfrog and green frog tadpoles showed no difference in critical thermal maxima (CT_{MAX}). Overall, both species had high CT_{MAX} values indicating that they can withstand relatively high pond temperature spikes. Indeed, these species occur in exposed, sunlit ponds and can experience maximum temperatures of $\sim 36^\circ\text{C}$ over

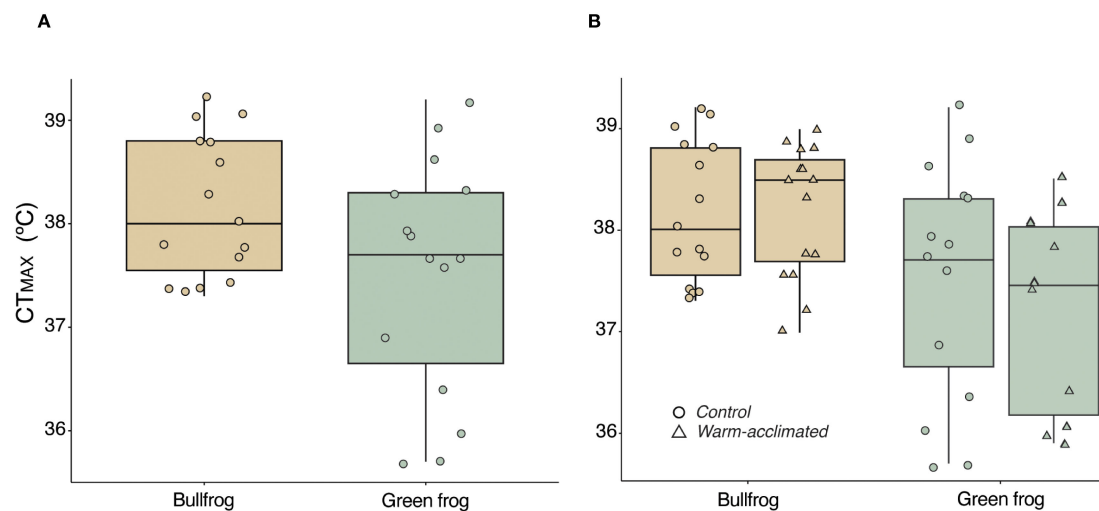


FIGURE 2

Boxplots from CT_{MAX} experiments on bullfrog and green frog tadpoles. **(A)** CT_{MAX} of bullfrog and green frog tadpoles after acclimation to 14°C. Green frogs have a qualitatively lower mean CT_{MAX} than bullfrogs. **(B)** Comparison of CT_{MAX} after cool and warm acclimation. There were no differences in acclimation capacity, however, average green frog CT_{MAX} declined slightly after warm acclimation suggesting that they may be marginally more sensitive to heat stress than bullfrogs.

several consecutive days in the summer (A. Shah, *unpubl. data*). Their CT_{MAX} are largely comparable to those measured for other temperate tadpoles (Duarte et al., 2012). However, after acclimating to a warmer temperature (20°C), the two species showed significant differences in their CT_{MAX} . These differences were driven by a decrease in CT_{MAX} in green frogs. Decreases in CT_{MAX} after acclimation to warm temperatures may indicate that green frogs are more sensitive to warming (e.g., Shah et al., 2017) and potentially have a lower capacity to acclimate to warmer conditions.

Indeed, during field collections, bullfrog tadpoles substantially outnumbered green frogs in shallow ponds that were several degrees warmer than the deeper ponds in the area (E. VanDenBerg, K. Jaynes, and A. Shah *pers. obs.*). In light of our results, this observation could be partly explained by the fact that green frog tadpoles are marginally more sensitive to warmer temperatures. However, other factors may also be at play. The higher abundance of bullfrog tadpoles in warmer ponds may additionally result from their ability to outcompete green frog tadpoles. If bullfrogs can perform (i.e., eat, grow, locomote) more effectively than green frogs at warmer temperatures, they may be better able to overtake and displace green frogs in warmer habitats (Mauro et al., 2022). For example, when bullfrogs were removed from an aquatic community, green frog abundance increased significantly, indicating that bullfrogs are superior competitors (Hecnar and M'Closkey, 1997). Testing the interaction between physiological performance and competitive differences in the two species across a range of temperatures was outside the scope of this study, but should be considered as a future research goal (Mauro et al., 2022).

A second potential physiological mechanism that may facilitate bullfrog invasiveness is thermal plasticity or acclimation (Mittan and Zamudio, 2019; Tepolt and Somero, 2014; Xue and Ma, 2020). Acclimation is predicted to enable species to persist across variable spatiotemporal thermal landscapes (Brattstrom and Lawrence, 1962;

Franklin et al., 2007; Sørensen et al., 2016) and adaptive plasticity can facilitate successful establishment in novel habitats (Bock et al., 2018; Corl et al., 2018; Mittan and Zamudio, 2019). We expected CT_{MAX} to increase after warm acclimation, particularly in bullfrog tadpoles. However, we found no differences in acclimation capacity between the two species. In fact, neither species showed any acclimation ability; i.e., their CT_{MAX} values remained largely unchanged after acclimation. One possible reason for this lack of plasticity may be that they already possess a relatively high basal tolerance for heat stress (average CT_{MAX} of both species after cool acclimation = 38°C). Some evidence suggests that due to physiological constraints, there may be a trade-off between basal thermal tolerance and the capacity of an organism to further increase its heat tolerance (Stillman, 2003; but see Birrell et al. 2023).

Additionally, acclimation ability can vary across populations (e.g., Cicchino et al., 2023) so, although acclimation capacity is limited in the populations tested in our study, other populations may well be able to acclimate to warmer conditions. For example, bullfrogs living closer to the warmer parts of the native range in North America may have greater acclimation capacity than their counterparts in the cooler parts. Alternatively, longer periods of acclimation to warmer temperatures or investigation of heat shock protein production (Zerebecki and Sorte, 2011) may reveal differences that were not seen in our experiment.

Conclusion

We hypothesized that intrinsic physiological tolerances between two congeners that differ in their invasive ability should vary. Our results revealed no major differences. In addition to being stronger competitors, we surmise that other factors, such as rapid evolution of thermal tolerance or combinations of responses to novel abiotic and biotic conditions may ultimately predispose bullfrog tadpoles to successfully persist in hotter habitats in the western U.S. We note

that with only two species (Garland and Adolph, 1994), and measuring traits in only the northern part of their range, we are limited in our ability to make strong conclusions about physiological differences. However, in addition to establishing a first step in measuring these differences, our study also provides a framework for testing other populations and multiple species in the future. Finally, investigating physiological tolerance in regions where bullfrogs were introduced, particularly those where green frogs have also established in the west, would be an important next step in understanding how physiological traits influence invasiveness.

Data availability statement

The original contributions presented in the study are publicly available. This data can be found here: FigShare, [dx.doi.org/10.6084/m9.figshare.30104779](https://doi.org/10.6084/m9.figshare.30104779).

Ethics statement

The animal study was approved by Institutional Animal Care and Use Committee (IACUC) at Michigan State University (project PROTO202200152). The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

EV: Data curation, Formal Analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. KJ: Conceptualization, Methodology, Visualization, Writing – original draft, Writing – review & editing. AS: Conceptualization, Formal Analysis, Funding acquisition, Methodology, Supervision, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declare that Generative AI was used in the creation of this manuscript. Chat GPT was used to help with R code syntax to make the map in Figure 1 and for the plots in Figure 2.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2025.1671218/full#supplementary-material>

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