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RESEARCH ARTICLE

Climatic niche evolution and speciation modes in the transisthmian *Alpheus* shrimps (Caridea: Alpheidae)

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Abstract

Aim: We studied the niche evolution and diversification modes in transisthmian *Alpheus* shrimps by examining the interplay between environmental niche divergence and conservatism in allopatric sister species. In a broader perspective, the current study analysed the evolution of climatic niche and the role of the environment in species diversification of *Alpheus* transisthmian shrimp.

Location: Atlantic and Eastern-Pacific oceans.

Taxon: *Alpheus* shrimps (Caridea: Alpheidae).

Methods: We assembled georeferenced occurrences for 33 species of *Alpheus* (with 24 sister species) from a time-calibrated molecular phylogeny. We modelled their ecological niches and assessed niche overlap through pairwise comparisons. Additionally, we performed phylogenetic reconstructions of the ancestral environmental niche, for each niche axis.

Results: Our results demonstrate that thermal tolerances, food availability and hydrodynamic forces were relevant environmental axes in evolutionary processes in transisthmian species of *Alpheus*. Among the 528 paired comparisons, we found that most niches were divergent, including in 12 clades formed by pairs of sister species (in only two of these clades were the niches fully equivalent). Phylogenetic reconstructions of ancestral niches showed an initial niche conservatism in all axes, with divergences intensifying in the last 12 million years.

Main Conclusions: We found evidence that confirms the relevance of the environmental changes that occurred in the West Atlantic and East Pacific for niche evolution in transisthmian *Alpheus* species, as well as for the emergence of some lineages. Our findings provide evidence for different modes of *Alpheus* species speciation in a period consistent with the closure of the Isthmus of Panama.

KEYWORDS

adaptive radiation, allopatric speciation, diversification, ecological niche modelling, niche overlap, sister species, transisthmian species

1 | INTRODUCTION

The question of how speciation occurs in megadiverse groups remains a fascinating and continually explored topic in evolutionary biology (Gavrilets & Losos, 2009; Hiller et al., 2019; Rundle & Nosil, 2005). Distinct mechanisms can favour the speciation process, which is contingent upon the geographic isolation of diverging populations and the resulting dynamics of gene flow (Papadopulos et al., 2011). Therefore, the existing biodiversity observed in megadiverse groups, like African cichlid fish (Ronco et al., 2021), ***Heliconius*** butterflies (Edelman et al., 2019), and *Anolis* lizards (Poe et al., 2018), stands as a compelling manifestation of evolutionary mechanisms and diverse processes contributing to speciation.

Since the mid-20th century, the prevailing consensus is that speciation primarily depends on populations with non-overlapping distributions (allopatry), largely attributed to geological or environmental barriers. Such distribution patterns could arise through vicariance (Mansion et al., 2009), extinction of intermediate zone populations (e.g., after local climate changes) (Wiens, 2004), or migration to isolated regions (Burbrink et al., 2019; Hertwig et al., 2013; Torres-Cambas et al., 2019). Depending on the isolation scenarios and the nature of barriers, be they physical or ecological, different modes of speciation can be identified. These modes are characterized by variations in levels of gene flow and the degree of similarity or divergence in ecological niches (Nosil, 2007; Wiens & Graham, 2005). Theoretical and empirical studies suggest that the limited gene flow between populations, imposed by barriers, can lead to population divergence and a process of speciation through different modes: [1] geographical vicariance, when the emergence of a physical barrier geographically divides two populations; [2] ecological vicariance, when environmental changes create an area with unsuitable conditions that impede gene flow between populations persisting in suitable areas. This disruption of gene flow leads to both geographical isolation and ecological divergence; [3] ecogeographical vicariance, when a physical barrier initially emerges and subsequently leads to adaptation of populations by changes in local environmental conditions; or [4] long-distance dispersal and establishment, when geographic isolation and limited gene flow lead to divergent populations after an exceptional dispersal event to isolated regions, independent of the emergence of vicariant barriers (Crisp et al., 2011). It is noteworthy that considering the speciation models [1–3], some temporal congruence between the speciation process and the emergence of the barrier is expected (Rincón-Barrado et al., 2021).

Thus, when speciation coincides temporally with the emergence of a physical barrier, a critical aspect of understanding the speciation modes lies in assessing the degree of niche conservatism exhibited by sister species (Kozak & Wiens, 2006). Phylogenetic niche conservatism (PNC) is the tendency of lineages to retain their ancestral ecological niche during speciation events (Harvey & Pagel, 1991). Notably, the closure of the Isthmus of Panama resulted in the isolation of distinct populations in the Caribbean and Pacific oceans; later, they differentiated into different species (transisthmian sister species) (Hurt et al., 2013; Knowlton et al., 1993; Knowlton & Weigt, 1998; Mathews et al., 2002). Nonetheless, the exact mechanism driving the appearance of these species remains ambiguous, leaving uncertain whether it was due to ecological speciation (resulting from niche divergence) or non-ecological speciation (stemming from niche conservatism).

In this study, we employ a comparative approach, analysing sister species and reconstructing ancestral niches, to investigate how environmental niche changes have influenced the radiation of ***Alpheus*** shrimp, a megadiverse genus that comprises 325 species (not including subspecies and uncertain taxonomic assignments) (WoRMS on May 6, 2022). These shrimps thrive in several habitats across multiple regions, exhibiting a wide geographic and ecological distribution, with a notable prevalence in coastal marine environments of tropical and subtropical areas (Elias et al., 2019; Hurt et al., 2021; Williams et al., 2001). The most recent estimates on the origin of this genus, based on multiple phylogenetic tree calibrations, corroborate a relatively ancient origin, in the Oligocene (see Hyžný et al., 2017), with great diversification from the Miocene (Hurt et al., 2021).

Considering the closure of the Isthmus of Panama, which led to the isolation of populations in environmentally distinct oceans, we propose that ecogeographic vicariance (ecological speciation), in which the resulting ***Alpheus*** sister species have divergent niches (Figure 1), should be the predominant mode of speciation. However, we also consider the geographic vicariance (non-ecological speciation) as an alternative mode to elucidate potential modes of speciation among ***Alpheus*** sister species (Figure 1). Thus, we intend to generate insights into the role of climatic niche in the diversification of transisthmian species within the genus ***Alpheus***. In a megadiverse group such as this, the role of niche divergence in speciation is expected to be high, suggesting low levels of niche conservatism. This prediction is particularly applicable to lineages undergoing rapid diversification through adaptive radiation, driven by ecological, behavioural, or physiological differentiation (Schluter, 2000).

2 | MATERIALS AND METHODS

2.1 | Species selection and phylogeny

To estimate the role of the climatic niche in *Alpheus* speciation, we chose to focus on Eastern Pacific (EP) and Western Atlantic (WA) species of *Alpheus*, an assemblage which has been intensively studied in terms of taxonomy (23 new species described in this region since 2007), divergence times (Hurt et al., 2009), and speciation (Hurt et al., 2013). Thus, we selected 33 species of ***Alpheus*** (with 24 sister species) from a dated ultrametric tree consisting of >50 *Alpheus* lineages based on three loci commonly used in alpheid phylogenetics (see supplementary material, for details about the construction and calibration of the phylogeny; Appendix S1). After loading the ultrametric and dated tree in R (v. 3.6.1), we deleted all lineages not considered for this study, and included one tip taxa per species (ape package, v.5.0, Paradis & Schliep, 2019). Consequently, we kept the dated phylogenetic distances for further analyses.

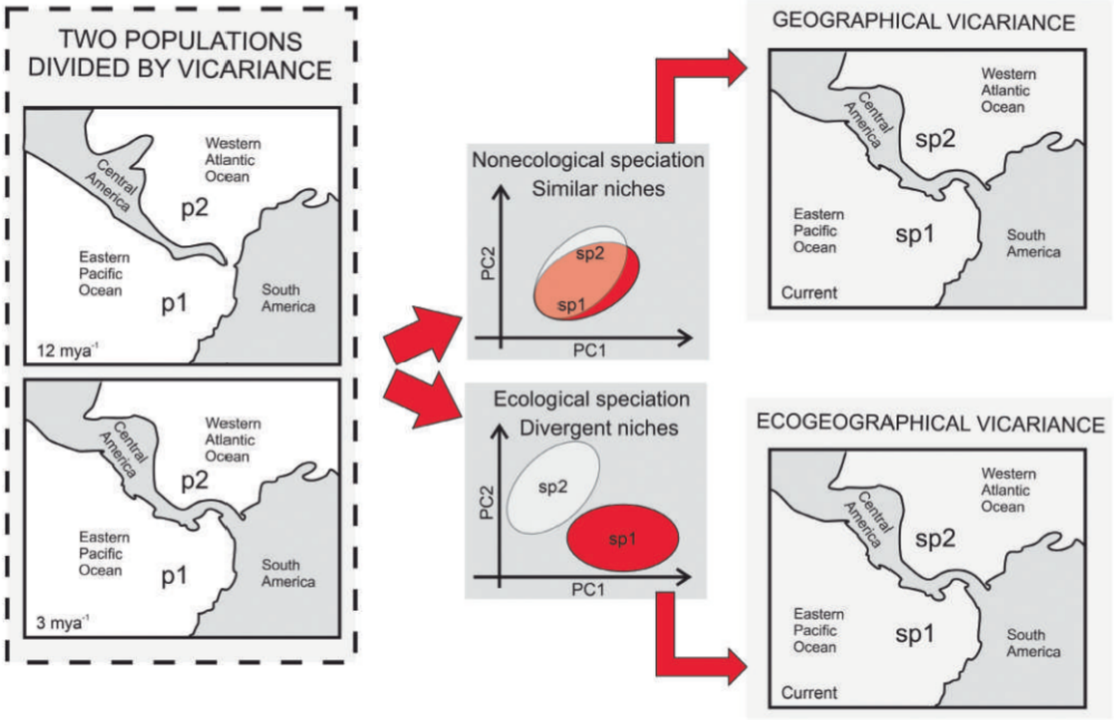


FIGURE 1 Conceptual framework supporting our hypotheses about speciation modes in megadiverse *Alpheus* shrimps. Populations (p) become isolated following a vicariant event; the divergence between transisthmian sister species (sp) takes place with niche divergence or retention of the ancestral niche (similar niches), leading to the proposition of two alternative hypothetical modes of speciation. PC, principal components of relevant environment data.

2.2 | Ecological modelling procedures

We obtained occurrence points for each of the selected species, totaling 14,692 occurrences from: three databases GBIF ($n=12{,}503$) (https://www.gbif.org/), OBIS ($n=1212$) (https://obis.org/), SPLINK ($n=127$) (https://specieslink.net/), specialized literature ($n=141$) and field collection ($n=709$, Hultgren, K., personal database). A rigorous cleaning procedure was applied to all occurrences, ensuring high data quality. This procedure involved excluding occurrences that were: (1) doubtful, such as those with latitude and longitude equal to zero; (2) outside the known native range, including occurrences in non-native oceans or points distant from the species' native marine provinces; (3) outside the extent of climate variables, characterized by imprecise points; and (4) outside the coastal marine regions delimited by polygons (Spalding et al., 2007). Because many species complexes of *Alpheus* have been taxonomically revised over the last two decades, we carefully examined all records against the taxonomic descriptions to ensure records were categorized with the current species name. Furthermore, the occurrence points were reduced to the same resolution as the environmental variables.

We obtained from Bio-Oracle (https://bio-oracle.org/) 22 environmental layers, representing mean and range values of 11 marine variables. After correlation and collinearity analyses, using Pearson's tests ($r \geq |0.65|$) and variance inflation factor ($\text{VIF}<5$), respectively, we selected eight environmental variables to be used in modelling the ecological niche of *Alpheus* shrimps. These variables include: mean currents velocity (Curr_Mean), mean dissolved molecular oxygen (Oxyg_Mean), nitrate range (Nitr_Range), mean primary productivity (Prod_Mean), mean salinity (Sali_Mean), silicate range (Sili_Range), temperature range (Temp_Range), and mean temperature (Temp_Mean).

Ecological niche models (ENMs) of *Alpheus* species were generated using the maximum entropy algorithm implemented in Maxent version 3.3.3 (Elith et al., 2011; Phillips et al., 2006). For this, we tested different combinations of MaxEnt parameters, such as regularization multiplier (rm) and features classes (fc) (ENMeval package, v.2.0, Kass et al., 2021; Muscarella et al., 2014). Twenty alternative models were generated with different combinations of rm (0.5–4.0) and fc (L = linear, Q = quadratic, and H = Hinge). The model with the best parameter adjustment was selected by comparing the AIC_c values generated for each alternative model. The selection of the best model was based on the criterion of $\Delta\text{AIC}=0$, following recommended practices in ecological niche modelling (Zurell et al., 2020). This rigorous parameter adjustment test aims to prevent both underfitting and overfitting of the models, ensuring optimal model performance. From the selection of the best fit of the MaxEnt parameters, we used the block method to partition the occurrences (Muscarella et al., 2014) to generate 10 ENMs replicates for each species. We used two metrics to evaluate the accuracy of the ENM of each species: the Area Under the Curve (AUC) (Fielding & Bell, 1997) and True Skill Statistics (TSS) (Allouche et al., 2006). The average model of the 10 replicates generated was used to predict the environmental suitability of each *Alpheus* species.

2.3 | Niche comparisons

To test the similarity between the niches occupied among the 33 alpheids under study, we compared all possible pairs of species, totaling 528 comparisons (see details about ENMs comparisons in Appendix S1). For these comparisons, we selected four environmental axes (Temp_mean, Temp_range, Curr_mean, and Prod_mean) that had the highest average percentage contributions to the generated models (see Supplementary Material, Appendix S1, Table S1.2). We use a 'PCA-env' approach (see Broennimann et al., 2012), to verify the overlapping of niches in e-space of each pair of species, using the Humboldt package and the concepts of niche and niche evolution (Brown & Carnaval, 2019).

The selected environmental variables were synthesized into two axes of a Principal Component Analysis (PCA). Subsequently, the PCA scores of each species were projected onto a grid of 100×100 cells. Then, to estimate the Schoener's D niche overlap metric, the smoothed occurrence density of each species along the grid was calculated by means of the Kernel density function. The Schoener's D ranges from 0 (completely non-overlapping) to 1 (completely overlapping) (Rödder & Engler, 2011). To assess its statistical significance ($\alpha = 0.05$), two randomization statistics, equivalence and background tests, were employed. These tests evaluated whether the niches were equivalent or divergent by generating random conditions in 1000 repetitions. Such a procedure was repeated using the entire distribution of the species being compared (Niche Overlap Test – NOT) and using only the environment shared by species (Niche Divergence Test – NDT) (Brown & Carnaval, 2019).

2.4 | Niche evolution

To examine the role of environmental niche evolution in the radiation of *Alpheus* shrimps, we initiated the analysis by generating predicted niche occupation (PNO) profiles for each of the 33 species across the four main environmental axes (phyloclim package, v.0.9.5, Heibl & Calenge, 2022). The PNOs were obtained to verify the probabilities of species occurrence (derived from MaxEnt) along the gradients of each environmental variable (bin n = 100). Then, we calculated the weighted average of the PNOs for each species and environmental axis.

To quantitatively assess the phylogenetic signal within each climatic axis of the niche, we employed various metrics. A strong phylogenetic signal indicates that ecological similarity among species is correlated with their phylogenetic relatedness (Losos, 2008). Here, a strong phylogenetic signal recorded for a given climate axis implies that such shrimp evolved along that axis in a manner similar to Brownian motion (BM), which involves minimal random change in any phylogenetic interval (see Losos, 2008). To investigate the phylogenetic signal, we first conducted simulations considering the topology of the *Alpheus* tree used in the present study. We simulated the behaviour of five different metrics, including Abouheif's Cmean, Moran's I, Blombergs K and K*, and Pagel's Lambda (phylosignal package, v.1.3, Keck et al., 2016). These simulations were performed under varying amounts of BM, with 1000 simulated solutions and 99 replicates for p-value estimation. Subsequently, using the PNO weighted average values of each species and each niche axis, we tested the phylogenetic signal within each axis. We obtained the values of the five metrics mentioned and determined their significance using a randomization test with 999 repetitions. Next, we ran correlograms to quantify the relationship between phylogenetic distance and each axis of the niche. Finally, we tested the Local Indicator of Phylogenetic Association (LIPA) for each tree species, using 'two-sided' alternative hypotheses.

To visualize niche evolution in *Alpheus*, we initially tested the fit of three evolutionary models: Brownian motion (BM), Ornstein-Uhlenbeck (OU), and Early-Burst (EB), individually for each environmental axis of the niche (geiger package, v.2.0.10, Pennell et al., 2014). We compared the fit of each model, for each environmental axis, through the values obtained from AIC_c (best model, $\Delta AIC = 0$). Once the best-fit evolutionary model was determined for each environmental axis, we performed ancestral reconstructions of the mean values of the four bioclimatic variables (phytools package, v. 0.4–60, Revell, 2012).

3 | RESULTS

The occurrence probability generated by PNOs (derived from MaxEnt models; see details about ENMs in Appendix S1) indicated that *Alpheus* shrimp can tolerate a wide range of mean temperatures, from 2 to 30°C (Figure 2), with some lineages preferring colder regions (0–5°C) and others preferring warmer regions (25–30°C) (Figure 2). Regions with minimal annual temperature variation (<1°C of Temp_range) are most suitable for alpheids. However, regions with Temp_range of ~5°C can also have some suitability for several lineages (Figure 2). *Alpheus* shrimp are specialists in two other environmental axes of significant contributions, Curr_mean and Prod_mean. Restricted ranges of these axes seem to be suitable for most species, with a similar occurrence probability among them (mean currents velocity $<0.25\,\text{m}^{-1}$ and mean primary productivity $<0.025\,\text{g.m}^{-3}.\text{day}^{-1}$, Figure 2).

Among the 528 pairwise comparisons made using NOT and NDT (as an example, Supplementary material, Appendix S1, Figure S1.4), the niche was fully equivalent in 233 comparisons, while in another 262 species pairs, the niches were fully divergent (Figure 3). Finally, for 33 pairs of species, although NOT indicated that the niches

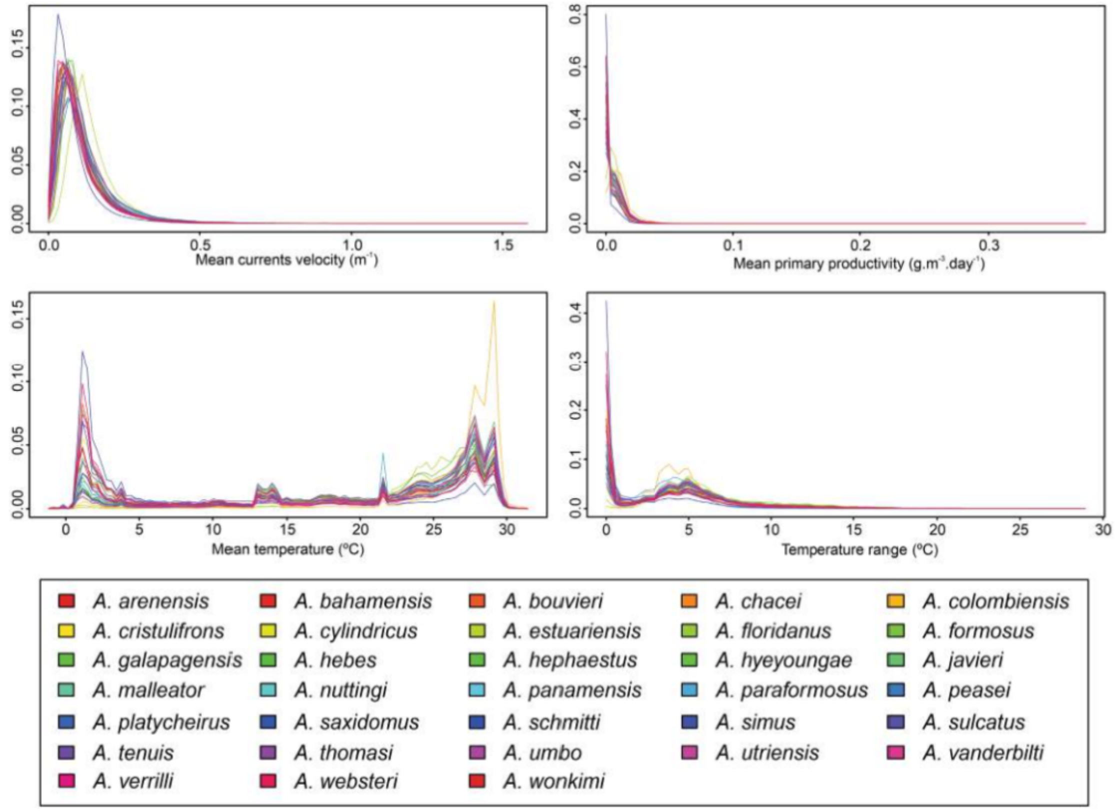


FIGURE 2 Models of predicted niche occupancy (PNO) of snapping shrimp species (*Alpheus*). Horizontal axes indicate the range of each environmental variable, while vertical axes indicate the probability of suitability for a given environmental value. PNO profile width indicates the species' environmental specificity or generality, with narrow profiles reflecting higher specificity. Overlapping peaks suggest that taxa have similar environmental tolerances, while non-overlapping peaks indicate different tolerances among species.

were not equivalent, the NDT results suggest that the niche occupied by the species is similar (Figure 3 and Supplementary Material, Appendix S2, Table S2.1). This comparison is especially interesting in 12 clades formed by pairs of sister species (clades 5, 8, 12, 13, 14, 17, 20, 22, 25, 28, 30, and 32) having each species restricted to different sides of the Isthmus of Panama (Atlantic or Pacific) (Figure 3a and Supplementary Material, Appendix S2, Table S2.1). In seven of those clades (5, 8, 12, 20, 22, 25, and 32) niche were recognized as divergent (Figure 3a and Supplementary Material, Appendix S2, Table S2.1). In only three of these clades (17, 28, and 30) niches were equivalent between sister species. Finally, for two other species pairs, niches were recognized as not equivalent (Figure 3a and Supplementary Material, Appendix S2, Table S2.1). The proportion of pairs with niche divergent was higher between sister species (59%) compared to non-sister species (49%) (Figure 3b).

The simulations generated to compare the performance of the different phylogenetic signal metrics, given the topology of the *Alpheus* tree used in the present study, yielded similar results across all five metrics (Supplementary material, Appendix S1, Figure S1.5). Moreover, such simulations revealed that the topology of the tree could generate a significant phylogenetic signal with a frequency higher than 40% for Brownian Motion (Supplementary material, Appendix S1, Figure S1.5b). Of the five metrics, no statistically significant phylogenetic signals were recovered in any of the environmental axes, except for mean current velocity (Curr_mean) in one of the metrics (Supplementary material, Appendix S1, Table S1.3). Considering the phylogenetic distance of the analysed species, significant correlations were not verified in any of the four environmental axes (Supplementary material, Appendix S1, Figure S1.6). Significant positive associations were verified in relation to phylogenetic distance and environmental similarity in several species, for all environmental axes, using LIPA analysis (Appendix S1, Figure S1.7). Most of these significant LIPA values were found in the species *A. schmitti*, *A. umbo*, *A. saxidomus*, *A. simus*, *A. thomasi*, and *A. paraformosus* (Appendix S1, Figure S1.7).

Based on the reconstruction of the ancestral niche, the niche of several *Alpheus* species diverged from that estimated for their ancestor during a period congruent with the speciation of the transisthmian

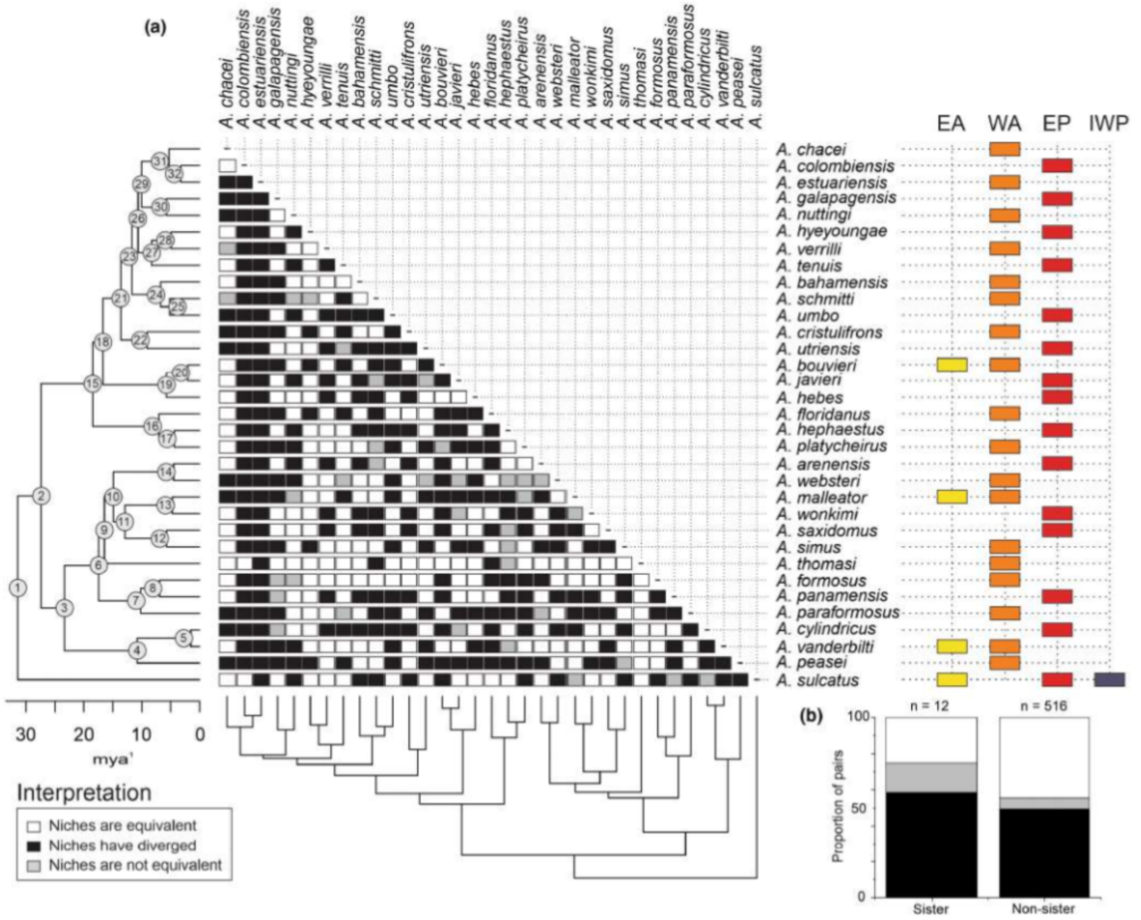


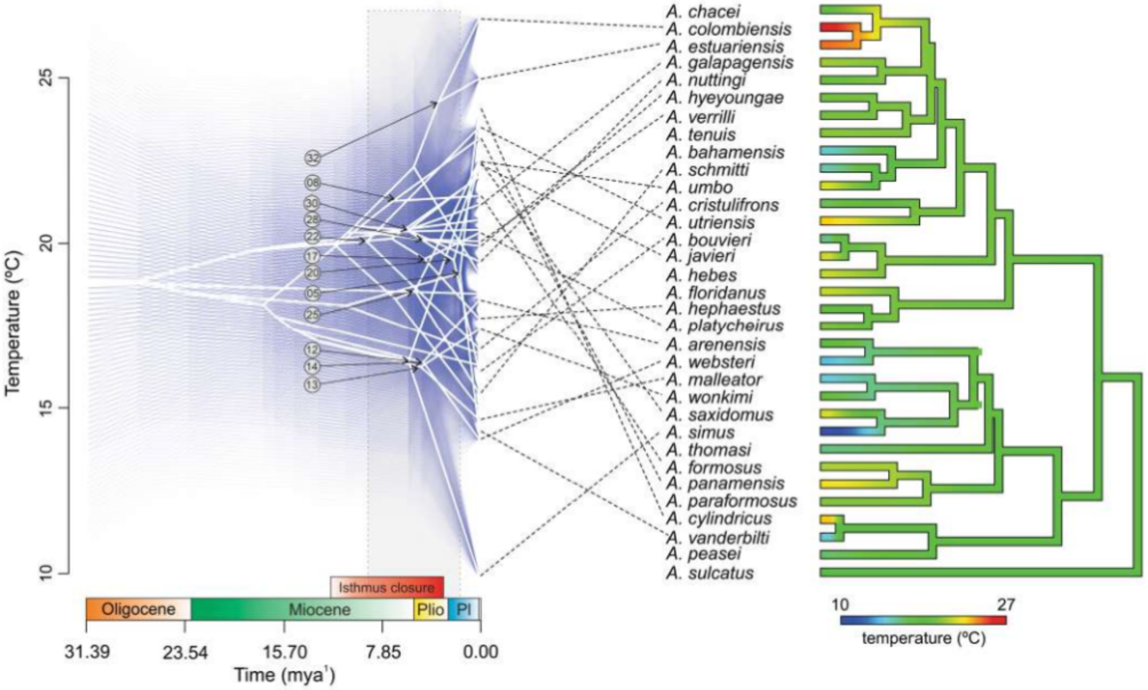
FIGURE 3 (a) Niche equivalence or divergence between each species pairs of snapping shrimp *Alpheus* represented in the phylogeny; (b) Proportion of pairs of niche equivalent, divergent and not equivalent for sister and non-sister species. Interpretation carried out by examining the results of the Niche Overlap Test (NOT) and Niche Divergence Test (NDT). Equivalency statistic and niche background statistic for each NOT and NDT can be found in supplementary materials (see Appendix S2, Table S2.1). EA, Eastern Atlantic; WA, Western Atlantic; EP, Eastern Pacific; IWP, Indo-West Pacific.

sister species (between 1.5 and 9 million years ago) (Figures 4 and 5). In general, the alpheid lineages showed an initial niche conservatism in all axes, with divergences intensifying in the last 12 million years (Figures 4 and 5). The lineages within clades exhibiting niche divergence (i.e., 5, 8, 12, 20, 22, 25, and 32) significantly contributed to niche evolution in *Alpheus* transisthmian species, displaying substantial divergences from the ancestral niche (Figures 4 and 5). In this context, the upper and lower limits of variation for all environmental axes were defined by species from clades 32 and 12, respectively (Figures 4 and 5). Such limits were reached through extremely divergent evolution of the niche between the lineages that form these clades (Figures 4 and 5). The Ornstein Uhlenbeck (OU) model was verified as the best-fit evolutionary model for the thermal axes of the niche, i.e., for mean temperature (Temp_Mean; AICc = 185.670) and temperature range (Temp_Range; AICc = 104.834) (Supplementary material, Appendix S1, Table S1.4). On the other hand, the Early Burst (EB) model was the best-fit evolutionary model for mean currents velocity (Curr_Mean; AICc = −169.090) and mean primary productivity (Prod_Mean; AICc = −277.820) (Supplementary material, Appendix S1, Table S1.4).

4 | DISCUSSION

The phylogenetic tree constructed for this study was highly supported (Supplementary material, Appendix S1, Figure S1.8) and corresponded to the last previous phylogeny of East Pacific/West Atlantic *Alpheus* (Williams et al., 2001), as well as more recent investigations of *Alpheus* species complexes. Our phylogeny recovered the same three major clades of Williams et al. (2001), as well as eight

(a) Temp_mean



(b) Temp_range

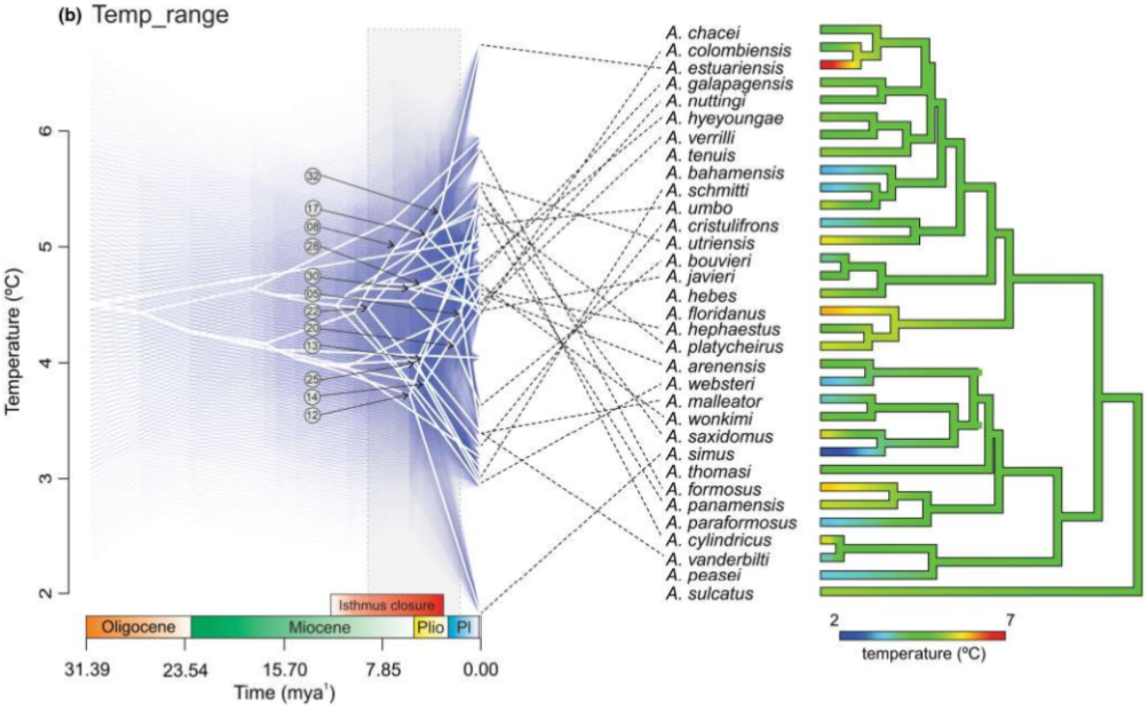
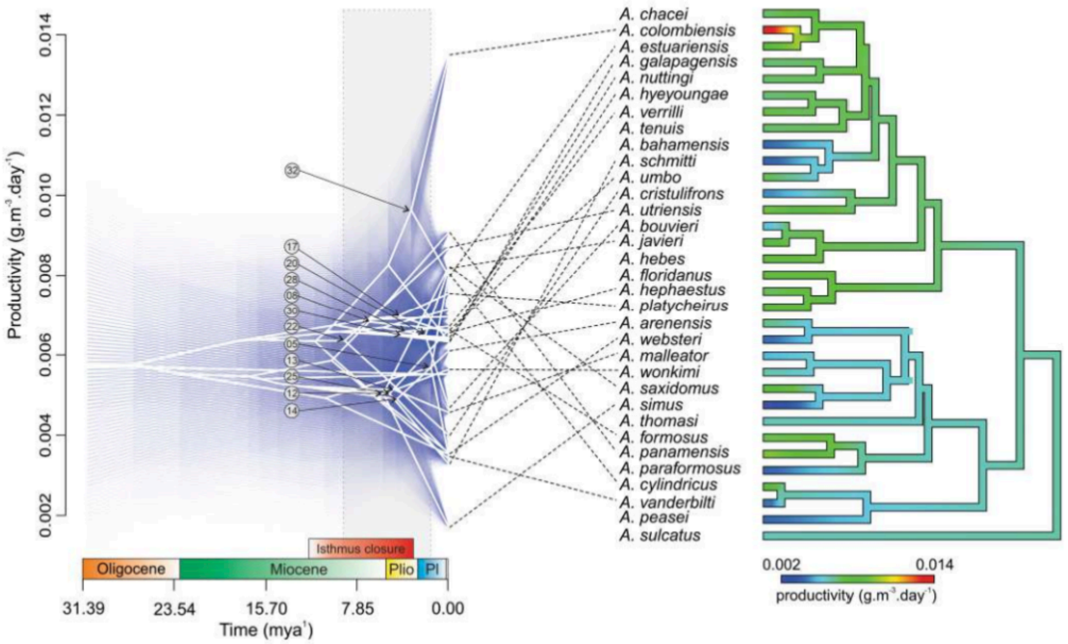


FIGURE 4 Reconstruction of ancestral niche based on the Ornstein-Uhlenbeck model (OU) for 33 species of *Alpheus* genus. (a) Temp_mean, temperature mean; (b) Temp_range, temperature range. Grey band represents the range of time that sister species diverged from their ancestral lineages. Arrows indicate each divergence of sister species from their ancestral lineages.

(a) Prod_mean



(b) Curr_mean

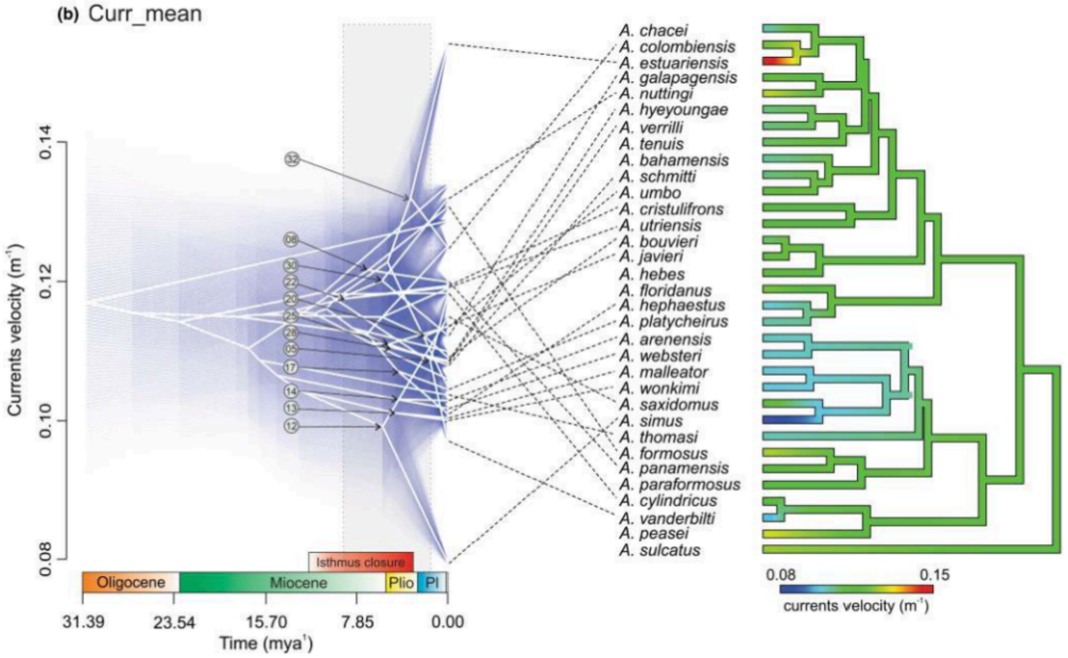


FIGURE 5 Reconstruction of ancestral niche based on the Early-Burst model (EB) for 33 species of *Alpheus* genus. (a) Prod_mean, primary productivity mean; (b) Curr_mean, current velocity mean. Grey band represents the range of time that sister species diverged from their ancestral lineages. Arrows indicate each divergence of sister species from their ancestral lineages.

well-established transisthmian pairs (Hurt et al., 2009; Knowlton et al., 1993; Knowlton & Weigt, 1998) or species complexes (Anker, 2012; Anker et al., 2008a, 2008b, 2008c, 2009; Bracken-Grissom et al., 2014) investigated over the last ~ two decades.

4.1 | Niche evolution

Our results suggest that thermal tolerances, food availability and hydrodynamic forces must be relevant in determining the limits of distribution, in the interactions between species, and consequently, in the evolutionary processes that were affected by such interactions in *Alpheus* transisthmian species. We found support for the influence of environmental transformations in the shallow marine ecosystems during the closure of the Isthmus of Panama on the evolutionary dynamics of niche among lineages of the *Alpheus* genus. Our results indicate that during the time period in which the Isthmus of Panama was closed, between ~12 and 3.5 million years ago (Mya[1]) (Hou & Li, 2018), there was also a significant evolution of the climatic niche of the *Alpheus* transisthmian species. The tectonic events associated with climate change and ocean currents that accompanied the closure of the Isthmus of Panama were responsible for major environmental changes in WA and EP (Leigh et al., 2014).

Regarding the niche axes investigated in the present study, temperature began to diverge between WA and EP earlier, in the mid-Miocene, compared to productivity, which appears to have diverged significantly around 4 million years ago, with the extinction of an area of seasonal upwelling in the Caribbean, consequently decreasing productivity in WA (Leigh et al., 2014). Furthermore, current patterns were completely modified after the complete closure of the Isthmus of Panama, that is, about 3 million years ago. Therefore, the best-fit evolutionary model found for average current velocity and average productivity is consistent with the scenario that such parameters diverged only earlier (around 3–4 Mya[1]) between WA and EP. Such regions presented contrasting environments after the complete closure of the Isthmus of Panama, including in the environmental variables related to the main axes used here to describe the niche of *Alpheus* species (temperature, productivity and current). The WA has lower productivity, lower salinity, higher surface temperature, narrower tidal range and more corals than the EP side (Lessios, 2008; Schwartz et al., 2012).

The thermic niche evolution of *Alpheus* transisthmian species seems to show a regression trend towards the mean, which was supported by the best fit to the Ornstein-Uhlenbeck. This pattern is observed, despite important divergences in the environmental profiles between lineages that were verified in the interval between 1.5 and 9 Mya[1] (see Figures 4 and 5). For example, the sister species *A. utriensis* and *A. cristulifrons* (with the split taking place in the late Miocene ~9 Mya[1]) presented divergent niches, with distinct specializations in the thermal axes, with *A. utriensis* occurring in regions of the eastern Pacific with warmer average temperatures, but with greater temperature range, compared to *A. cristulifrons* which occurs in the western Atlantic. This result shows that environmental changes that occurred between the Late Miocene and Pliocene were important for the evolution of this group of shrimps. In this context, the Neogene was marked by several geological and climatic events with major impacts on marine fauna, such as: [1] tectonic events in the Andes region, which modified ocean circulation patterns, nutrient distribution, and climatic conditions along the west coast of South America (Boschman, 2021; Garzione et al., 2008; Sepulchre et al., 2010; Strecker et al., 2007); [2] the opening of the Gibraltar Strait (during the Pliocene period, around 5.33 Mya[1]), which reconnected the Mediterranean Sea to the Atlantic Ocean and with the end of Messinian salinity crisis (between 7.24 and 5.33 Mya[1]) (Garcia-Castellanos et al., 2009; Hernández-Molina et al., 2014); [3] climate change and Antarctic glaciation, which also caused changes in sea levels (De Blasio et al., 2015; Jakob et al., 2020; Lazarus et al., 2014; Marschalek et al., 2021; Trubovitz et al., 2020); in addition to [iv] closure of the Isthmus of Panama, which in the present study was tested as one of the main events that affected the evolutionary history of the genus *Alpheus*, corroborating with suggestion of other studies that this event had a great impact on the diversification of marine fauna (Baraf et al., 2019; Hiller & Lessios, 2020; Hou & Li, 2018; Hurt et al., 2013; Leigh et al., 2014; Thacker, 2017).

Hence, our findings substantiate the assertion that environmental fluctuations occurring between 1.5 and 9 million years ago (Mya[1]) influenced the evolutionary trajectory of climatic niches in transisthmian *Alpheus* species. Of particular significance is the observation that lineages adapting to climatic limits markedly different from the majority of lineages (see clades 12 and 32; Figures 4 and 5), seem to have split during a temporal interval aligned with the complete closure of the Isthmus of Panama, estimated at approximately 3 million years ago (Mya[1]).

4.2 | Speciation modes

Previous studies have already considered the importance of closure of the Isthmus of Panama for the diversification of *Alpheus* transisthmian species (e.g., Hurt et al., 2009; Knowlton et al., 1993; Knowlton & Weigt, 1998). However, the role of the environment in diversification has not been tested, which made it difficult to advance our understanding of speciation modes. We found a predominance of climate niche divergence among the species analysed in this study, with most sister species pairs supporting the relevance of the environment in the speciation of *Alpheus* transisthmian species (i.e., ecogeographical speciation) leading to adaptive radiation (Table 1). On the other hand, we also verified some prevalence of speciation modes that consider niche conservatism (i.e., geographical vicariance) that configure as non-adaptive radiations. By relating cases of niche equivalence or divergence of sister species, we found support for our two alternative hypotheses with two different modes of speciation acting during the diversification process in *Alpheus* (see Table 1).

Furthermore, our results support climatic niche divergence for seven pairs of sister species (clades 5, 8, 12, 20, 22, 25, and 32),

TABLE 1 Sister species in *Alpheus* and the most likely mode of speciation supported by spatial, temporal congruence with closure of the Isthmus of Panama, and environmental niche evidence.

Clade	Species	Climatic niches	Speciation mode
5	*A. cylindricus* *A. vanderbilti*	Divergent	Ecogeographical vicariance
8	*A. panamensis* *A. formosus*	Divergent	Ecogeographical vicariance
12	*A. saxidomus* *A. simus*	Divergent	Ecogeographical vicariance
13	*A. malleator* *A. wonkimi*	Not Equivalent	Geographical vicariance[a]
14	*A. arenensis* *A. websteri*	Not Equivalent	Geographical vicariance[a]
17	*A. hephaestus* *A. platycheirus*	Equivalent	Geographical vicariance
20	*A. bouvieri* *A. javieri*	Divergent	Ecogeographical vicariance
22	*A. cristulifrons* *A. utriensis*	Divergent	Ecogeographical vicariance
25	*A. schmitti* *A. umbo*	Divergent	Ecogeographical vicariance
28	*A. hyeyoungae* *A. verrilli*	Equivalent	Geographical vicariance
30	*A. galapagensis* *A. nuttingi*	Equivalent	Geographical vicariance
32	*A. colombiensis* *A. estuariensis*	Divergent	Ecogeographical vicariance

[a] The NOT and NDT results do not support the hypothesis of divergent evolution.

which are currently geographically isolated and separated by the Isthmus of Panama (allopatric distribution) (Anker et al., 2008a, 2008b, 2008c, 2009; Hurt et al., 2009; Knowlton et al., 1993). The disparities observed were substantiated through the application of the NDT test (Niche Divergence Test), revealing non-equivalence in the niches of species comprising each sister pair. Such results supporting the hypothesis that their fundamental niches are the result of divergent evolution (Brown & Carnaval, 2019). For these seven pairs of sister species our findings support ecogeographic speciation (Table 1). In this speciation mode, lineage divergence is initially driven by geographic isolation (allopatric), but later divergent natural selection in one or both allopatric populations drives differentiation, due to changes in local environmental conditions (Czekanski-Moir & Rundell, 2019). In this case, the emergence of the Isthmus of Panama generated the geographic isolation and the environmental changes that occurred in WA and EP after such a vicariant event generated different ecological pressures for populations at different times. Importantly, speciation can be faster or slower depending on the force of adaptation (Couvreur et al., 2011).

For three other species pairs with allopatric distributions (clades 17, 28 and 30), our results indicated a climatic niche equivalence. However, for the other two pairs of remaining sister species (clades 13 and 14), the NOT and NDT results support that their current niches are not equivalent, however, these results also do not support the divergent evolution hypothesis; rather, the differences are simply the result of different access to environments (Brown & Carnaval, 2019). Therefore, for these five clades, our results support the proposal of a geographical vicariance mode of speciation (non-ecological) (Table 1). In this mode, the speciation is driven by isolation and accumulation of mutations between populations separated by a barrier, which leads to reproductive incompatibility but not strong ecological differentiation (Czekanski-Moir & Rundell, 2019). Species divergence of these three clades from their ancestors was earlier compared to the time to divergence of the species for which we suggest ecogeographic speciation. Several studies have found evidence of non-adaptive radiation, which does not depend on divergent ecological selection (e.g., Lee-Yaw & Irwin, 2015; Maestri et al., 2017; Reaney et al., 2018), including in the marine environment (Lessios, 2008; Meyer, 2003).

5 | CONCLUSION

The current study analysed the evolution of climatic niche and the role of the environment in species diversification of *Alpheus* transisthmian shrimp. We evaluate niche similarity or divergence providing evidence for different modes of speciation in a period consistent with the closure of the Isthmus of Panama. Therefore, we suggest that the diversification into transisthmian species occurring from the Late Miocene to the Pliocene (between 9 and 1.5 Mya[1]) exhibits elements of adaptive and non-adaptive radiation, in allopatric sister species pairs. Thus, our results highlight the relevance of the environmental changes that occurred in the WA and EP for the niche evolution of this shrimp group, as well as for the emergence of some lineages.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicting or competing interests.

DATA AVAILABILITY STATEMENT

The environmental variables used as predictors and the species' occurrence points can be found in online repository (10.5061/dryad.bk3j9kdk8). More information is available in Appendix S1 Information. Details of the sequences used to generate the phylogeny in this study are available in Appendix S3. All GenBank accession numbers are listed in Appendix S3.

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BIOSKETCH

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SUPPORTING INFORMATION

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

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