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Short Communication

Chromosomal diversity in tropical reef fishes is related to body size and depth range ☆

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ABSTRACT

Tropical reef fishes show contrasting patterns of karyotypic diversity. Some families have a high chromosomal conservatism while others show wide variation in karyotypic macrostructure. However, the influence of life-history traits on karyotypic diversity is largely unknown. Using phylogenetic comparative methods, we assessed the effects of larval and adult species traits on chromosomal diversity rates of 280 reef species in 24 families. We employed a novel approach to account for trait variation within families as well as phylogenetic uncertainties. We found a strong negative relationship between karyotypic diversity rates and body size and depth range. These results suggest that lineages with higher dispersal potential and gene flow possess lower karyotypic diversity. Taken together, these results provide evidence that biological traits might modulate the rate of karyotypic diversity in tropical reef fishes.

1. Introduction

Chromosomal rearrangements may promote evolutionary diversification via reproductive isolation (Kirkpatrick, 2010; Rieseberg, 2001; White, 1978). Chromosomal rearrangements, as inversion and fusion, suppress the recombination and/or lead to a underdominance in heterokaryotypes (Hooper and Price, 2015). Fish families of tropical reefs show contrasting levels of karyotypic diversity (Galetti et al., 2000). Some lineages exhibit strong chromosomal conservatism (e.g., Haemulidae, Carangidae), whereas others vary substantially in their karyotypic macrostructure (e.g. Gobiidae, Pomacentridae) (Molina et al., 2014a). However, the factors leading to low or high rates of chromosomal diversity have not been clearly identified.

Previous cytogenetic studies show that some marine fish lineages have karyotypic characteristics, such as the presence of repeated sequences or heterochromatin content, that favor the occurrence of certain types of chromosomal rearrangements (Molina et al., 2014b). However, the fixation of a given chromosomal mutation will mostly depend on its adaptive value, on deme size, and on migration rates between populations (Hooper and Price, 2015; King, 1995; Guerrero and Kirkpatrick, 2014).

Tropical reef fishes feature a wide range of dispersal abilities; some species are endemic to small islands while others are found in entire oceanic basins (Luiz et al., 2013). Body size is strongly correlated with dispersal ability in a variety of organisms (Hillman et al., 2014; Pyron, 1999). However, in marine environments, most organisms disperse as larval propagules through ocean currents (Shanks et al., 2003). Therefore, a broad-scale analysis of larval and adult traits linked to dispersal ability is essential to assess the factors driving of karyotypic diversification in reef fishes (Molina et al., 2014b).

Here, we compile a dataset of traits reported from larval and adult species of tropical fish families (Luiz et al., 2013) in addition with chromosomal information (Arai, 2011) to investigate the effects of life-history traits on rates of karyotypic diversity (rKD). To address this question we employ a suite of phylogenetic comparative methods using a novel approach to account for both phylogenetic and trait uncertainty and leveraging recent insights on the evolutionary diversification of fishes made available by broad-scale molecular phylogenetic analyses (Betancur-R et al., 2013, 2015).

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2. Methods

2.1. Estimation of rates of karyotypic diversity

The main mechanism of chromosomal rearrangement in marine fishes is pericentric inversion, which alters the karyotype fundamental number (number of chromosome arms or NF). However, changes in chromosome number due to Robertsonian fusions also occur (Molina et al., 2014b). We collected chromosomal information on diploid ($2n$) and fundamental numbers (FN) of 280 species belonging to 24 families of reef fishes (~25% of reef fish families) (Arai, 2011). We only included those species for which the phylogenetic position of the genus, was known. The species belong to 82 genera that are represented in the most recent time-calibrated phylogeny of ray-finned fishes (Betancur-R et al., 2013, 2015). The species that were not included in the phylogenetic hypothesis of Betancur-R et al. (2015), were randomly incorporated in the genus node into which they belong using a recent approach (Martins et al., 2013; Appendix I). Chromosomal data of species for which information of their generic phylogenetic position was unavailable, were not considered.

We analyzed the time and mode of evolution of $2n$ and FN through the phylogeny using the software BAMM 2.3.0 (Rabosky et al., 2014b). This software employs the reversible jump MCMC method to find evolutionary rates throughout the tree that best explain the distribution of species $2n$ and FN. We thus obtained estimates of karyotypic diversity rate (rKD) of $2n$ (rKD-$2n$) and FN (rKD-FN) for each species (see Rabosky et al., 2014a,b). Convergence rates of Markov chains were assessed through effective sample size using the *coda* package vs.0.17-1 (Martyn et al., 2015) in R 3.0.2. Effective sample size larger than 200 was considered as a satisfactory performance of BAMM simulations (Rabosky et al., 2014a).

2.2. Effect of biological traits on karyotypic diversity rate

We considered the following larval and adult traits related to dispersal potential and diversity of habitat use: (i) pelagic larval duration (PLD; i.e. the time between spawn and larval settlement); (ii) spawning mode (benthic/pelagic eggs); (iii) adult body size (maximum total length); and (iv) depth range. All trait data came from Luiz et al. (2013) (Table S1). For continuous variables, we calculated a mean value and standard error per family and log-transformed the data. In all families the majority of species had the same spawning mode. To analyze the effect of biological traits on rKD-$2n$ and rKD-FN, we estimated the mean rKD for each family from the tip values obtained with the BAMM software. Analyses were performed using phylogenetic generalized least squares regressions (PGLS) with phylogenetic signal (λ) estimated through maximum likelihood with the Caper package vs. 0.5.2 (Orme et al., 2014) implemented in R 3.0.2. We generated 100 phylogenetic trees by randomizing the species with phylogenetic uncertainty, which were used in 100 PGLS analyses (hereafter "tree replicates") to account for phylogenetic uncertainties (Martins et al., 2013; Rangel et al., 2015). Similarly, in order to account for trait variability among species within a family, for continuous traits (i.e. depth range, PLD and body size), we randomly picked a value within the standard error of the mean (hereafter "trait replicates"). We randomized trait values 500 times, leading to 50,000 models (tree replicates × trait replicates) (Appendix I). In order to evaluate the models we considered the mean and standard deviation of model results (mean p-value, r^2, AICc and estimate) across the 50,000 replicates. We also calculated the deviation in model results separately for tree replicates and trait replicates. All R scripts have been posted on an online repository (https://github.com/caterinap/ChromDiv).

3. Results and discussion

The rate of karyotypic diversity varied broadly among different lineages. The highest values in rKD-$2n$ and rKD-NF were observed in Apogonidae, and lowest values in Haemulidae (Fig. 1, Table S1). Two trends in karyotypic evolution of Actinopterygii fishes have been observed, with some lineages showing slow karyotypic evolution, and others showing fast chromosomal changes (Molina et al., 2014a). These patterns are clearly observed in our mapping of rKDs of tropical reef fishes (Fig. 1). In general, our estimated rKDs are congruent with patterns of karyotype diversification postulated by previous authors (Galetti et al., 2000; Molina et al., 2014a).

It is worth noting that some families show contrasting patterns for rKD-$2n$ and rKD-FN with a low rate of fusion/fission; but high rate of fixation of chromosomal inversions rearrangements; e.g., Serranidae and Pomacentridae (Fig. 1; Table S1). Mechanisms such as genetic drift, divergent selection and/or meiotic drive regulate the fixation of chromosomal rearrangements (Dover, 2002; Galetti et al., 2000; Molina et al., 2014a, 2014b; Villena and Sapienza, 2001; White, 1978). However, the biological causes that lead different lineages to show differential rates of chromosomal rearrangements have not been thoroughly analyzed.

In PGLS analysis, rKD-FN showed a significant correlation with body size, (PGLS, $b = -1.42 \pm 0.11$, $r^2 = 0.29 \pm 0.04$, $p < 0.007 \pm 0.005$) and depth range (PGLS, $b = -0.84 \pm 0.06$, $r^2 = 0.20 \pm 0.02$, $p < 0.03 \pm 0.01$) (Table 1) (Fig. 2). The rKD-FN/body size was the best fitting model showing the lower AICc value (Table 1). Conversely, the rKD-$2n$ did not show any significant relationship with the considered traits. This lack of significance is not surprising given that the main mechanism of karyotypic diversity that has been observed in marine fishes is pericentric inversions that alter NF (Molina et al., 2014a, 2014b).

Our results show that adult life-history traits (but not larval traits) are linked to dispersal ability and rate of karyotypic diversity (rKD). The establishment of differentiated karyotypes may be a consequence of lower dispersal ability and reduced vagility of species, leading to faster fixation of chromosomal rearrangements (de Sena and Molina, 2007; Molina and Galetti, 2004). Indeed, high gene flow among populations is only possible when populations disperse to new areas and become successfully established. Therefore, traits that allow higher survival of adults can facilitate gene flow, further preventing chromosomal rearrangements. In addition, the establishment of chromosomal rearrangements can reinforce isolation reducing gene flow between hybridizing species and producing inviable progeny that would contribute to the persistence of species (Navarro and Barton, 2003; Rieseberg, 2001). We observed that larger species occupying a broader range in the water column have lower rKD-FN (Table 1). Body size is strongly correlated with distributional range since larger species tend to show a higher dispersal potential (Luiz et al., 2013). On the other hand, depth range is related to the occupation of the vertical water column. This agrees with the general idea that lineages with higher dispersal potential and gene flow possess lower karyotypic diversity (de Sena and Molina, 2007). Chromosomal changes, may play an important role in controlling recombination indexes as they may protect genetic combinations that provide advantages in certain habitats or environments (Kirkpatrick and Barton, 2006; Kirkpatrick, 2010). In the marine realm, phylogeographic barriers, such as water currents or large geographic distances, are all relatively permeable (Cowman and Bellwood, 2013). Genetic divergences are thus more likely to take place in allopatry (e.g., sister species separated by the Isthmus of Panama). The lack of insurmountable barriers in tropical seas, probably favors gene flow while preventing the fixation of adaptive chromosomal characteristics. In marine fishes, chromosomal inversions have been shown