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Sexual Dichromatism Is Decoupled from Diversification over Deep Time in Fishes

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ABSTRACT: Sexually selected traits have long been thought to drive diversification, but support for this hypothesis has been persistently controversial. In fishes, sexually dimorphic coloration is associated with assortative mating and speciation among closely related species, as shown in classic studies. However, it is unclear whether these results can generalize to explain diversity patterns across ray-finned fishes, which contain the majority of vertebrate species and 96% of fishes. Here, we use phylogenetic approaches to test for an association between sexual dichromatism and diversification rates (speciation minus extinction) in ray-finned fishes. We assembled dichromatism data for 10,898 species, a data set of unprecedented size. We found no difference in diversification rates between monochromatic and dichromatic species when including all ray-finned fishes. However, at lower phylogenetic scales (within orders and families), some intermediate-sized clades did show an effect of dichromatism on diversification. Surprisingly, dichromatism could significantly increase or decrease diversification rates. Moreover, we found no effect in many of the clades initially used to link dichromatism to speciation in fishes (e.g., cichlids) or an effect only at shallow scales (within subclades). Overall, we show how the effects of dichromatism on diversification are highly variable in direction and restricted to certain clades and phylogenetic scales.

Keywords: diversification, fishes, sexual selection, speciation, color, phylogenetic scale.

Introduction

A major goal in evolutionary biology is to explain why some clades have more species than others (Wiens 2017). Fundamentally, new species are added to a clade through speciation and removed through extinction. Therefore, an important explanation for variation in richness among clades is that they differ in their net diversification rates (speciation minus extinction rates).

Diversification rates can be influenced by organismal traits that affect the probability of speciation or extinction. Darwin (1871) first observed that many of the most obvious differences between closely related species are in traits involved in courtship (Ritchie 2007), including the bright colors in males of many species (fig. 1). This observation led to the influential hypothesis that sexually selected traits play a role in the origin of new species (Boughman 2014). Classic papers proposed that sexual selection drives speciation through assortative mating (Lande 1981; West-Eberhard 1983). However, several additional mechanisms could also help explain how sexual selection could increase net diversification rates (Tsuji and Fukami 2020). For example, sexual selection may drive speciation through postzygotic isolation (Irwin 2020) or by facilitating ecological divergence (Albert et al. 2008). Sexual selection can also reduce extinction by helping populations adapt to changing environments (Lorch et al. 2003) or purge mutation loads (Lumley et al. 2015).

Conversely, sexual selection can also decrease net diversification rates. Sexual selection can inhibit speciation through negative assortative mating (Servedio and Burger 2014) or when sexes compete for resources (Bolnick and Doebeli 2003). If sexually dimorphic traits increase individual mortality, then sexual selection can drive species to extinction (Promislow et al. 1992; Martins et al. 2018). In sum, sexual selection may increase or decrease net diversification rates of clades through several mechanisms that act on speciation or extinction.

Comparative studies testing for an association between sexually selected traits and diversification rates have found mixed results. Sexual dichromatism was first found to be positively related to species richness and diversification on the basis of comparisons of sister clades of passerine birds (Barraclough et al. 1995). However, subsequent studies in birds found no such relationship (Morrow et al. 2003; Huang and Rabosky 2014). Studies in other animal clades are similarly divided on whether sexual selection increases, decreases,

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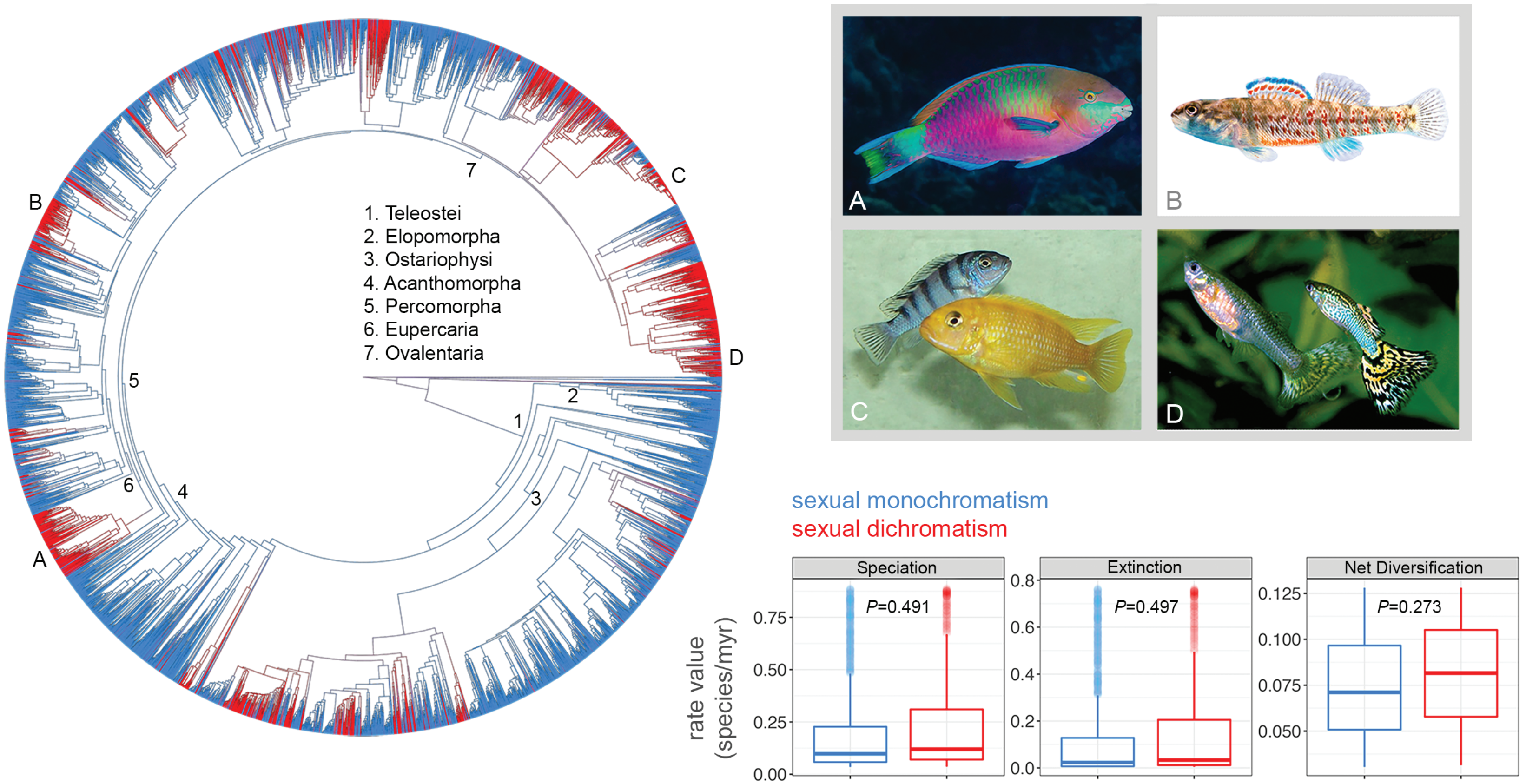


Figure 1: Sexual dichromatism and diversification across ray-finned fishes. An ancestral reconstruction of sexual dichromatism was estimated using the best-fit hidden state speciation and extinction model (table A14) on a phylogeny of all ray-finned fishes (Rabosky et al. 2018). Representative clades with prior work on sexual dichromatism and assortative mating, reproductive isolation, and/or diversification are shown in photographs: parrotfishes (Kazancıoğlu et al. 2009; *A*), darters (Mendelson 2003; *B*), cichlids (Seehausen et al. 1997; *C*), and guppies (Furness et al. 2019; *D*). Across ray-finned fishes, there were no significant differences in rates between sexually monochromatic and dichromatic species (table A15). Rates for monochromatic species are shown on the left in blue; rates for dichromatic species are shown on the right in red. Boxplots summarize rates for individual species, including medians, first and third quartiles, and outliers (outside the 95% confidence interval). Photograph credits: François Libert (*A*); Daniel MacGuigan (*B*); Wikimedia user Ged~commonswiki, public domain (*C*); Wikimedia user Marrabbio2, CC BY-SA 3.0 (*D*).

or has no effect on diversification (Kraaijeveld et al. 2011; Tsuji and Fukami 2020).

One possible explanation for these conflicting results is the different taxonomic scales among studies. A meta-analysis (Kraaijeveld et al. 2011) posited that studies at smaller scales (e.g., studies within bird genera) were more likely to recover a positive effect of sexual selection on diversification than studies of older clades (bird families). These authors suggested that this occurs because extinction prunes many of the species gained by speciation through sexual selection, so these species are not observed. A study that attempted to parse out the effects of taxonomic scale found no relationship between sexual dichromatism and speciation rates across all birds and none within most families (Huang and Rabosky 2014). Furthermore, a subsequent study in birds compared diversification rates among recently diverged sister species pairs and still found no relationship between dichromatism and speciation rates (Cooney et al. 2017). Thus, empirical evidence for this scaling hypothesis remains limited. However, it has been tested only in birds so far.

Despite uncertainty in other groups, current evidence for a positive effect of sexual dichromatism on speciation in ray-finned fishes is compelling (Kraaijeveld et al. 2011). With ~31,000 species, ray-finned fishes (Actinopterygii) contain ~96% of all fish species and ~50% of all vertebrates (Helfman et al. 2009). There is strong evidence that species-specific, sexually dichromatic colors are under sexual selection in fishes (Kodric-Brown 1990, 1998). In addition, male colors have been linked to assortative mating and/or reproductive isolation in several clades, including classic studies in cichlids (Seehausen et al. 1997, 2008; Elmer et al. 2009), darters (Mendelson 2003; Martin and Mendelson 2014), guppies (Houde and Endler 1990), and sticklebacks (Boughman 2001). Furthermore, sexual dichromatism has been linked with diversification over macroevolutionary timescales in cichlids (Wagner et al. 2012; McGee et al. 2020), parrotfishes (Kazancıoğlu et al. 2009; Choat et al. 2012), poeciliids (guppies and allies; Furness et al. 2019), and sunfishes (Smith et al. 2015). Most notably, sexual dichromatism helps explain why African cichlids have the fastest diversification rates among all animals (McGee et al. 2020). If the factors that promote reproductive isolation among populations also explain diversification rates over deeper timescales, then sexual dichromatism could help explain the striking differences in species diversity among ray-finned fish clades. For example, actinopterygian orders range from one to >4,000 species (table A1; tables A1–A28 are available online; Rabosky et al. 2018; Froese and Pauly 2019).

Here, we investigate the effect of sexual dichromatism on diversification rates across ray-finned fishes. This goal was shared by two previous studies that used sister clade comparisons to address diversification (Mesnick 1996; Mank 2007). Both studies found that groups with a greater prevalence of sexual dimorphism (in color and other features) were generally more species rich, which is consistent with faster diversification. However, the sister clade approach necessarily limits comparisons to only those groups that vary in the presence of dimorphism. Collectively, these two studies included 30.9% of ray-finned fish orders and 11.6% of families (Froese and Pauly 2019). This limitation may bias the range of diversification rates seen among monomorphic groups (e.g., ascertainment bias; Beaulieu and O'Meara 2018), potentially leading to incorrect inferences about the influence of sexual selection on diversification overall.

We improved on previous analyses of ray-finned fishes in three ways. First, we collected data on sexual dichromatism for 10,898 species, including 35% of described species, 89% of families, and 100% of orders (following taxonomy of Rabosky et al. 2018). Our data set is the largest on sexual dichromatism compiled for any animal group. Second, we used methods that separately estimate rates of speciation, extinction, and net diversification rather than using species richness as a proxy for diversification. Third, we performed analyses at three scales: across all ray-finned fishes, within clades in which sexual dichromatism evolved, and within smaller subsets of these clades. We also perform analyses that compare rank-free clades for a range of clade ages. By sampling broadly across taxa and scales, we can identify the scales at which sexual dichromatism drives diversification, if at all.

Material and Methods

Literature Search

We conducted an extensive literature search on the presence or absence of sexual dichromatism in actinopterygian fishes. We targeted information for those species that were represented in the phylogeny used (Rabosky et al. 2018; text A1; table A1; texts A1–A5 are available online). Our search was conducted from November 1, 2017, to June 1, 2019. We used the package rfishbase v.2.99 (Boettiger et al. 2012) to reconcile synonyms across literature sources. We focused on color differences over other forms of sexual dimorphism because these differences are (1) relatively straightforward to identify, (2) often reported when they exist (see below), and (3) linked to assortative mating, reproductive isolation, and/or diversification in many previous studies (see above).

Sexual dichromatism was defined here as any reported difference in color between the sexes at any stage in the adult life cycle, including differences in color pattern or intensity. This definition includes permanent and temporary dichromatism (Kodric-Brown 1998) as well as color changes associated with sex change. This definition is agnostic regarding the degree of difference between the sexes, the mechanistic basis for color (e.g., melanic, carotenoid), and whether males or females are more colorful. We chose this definition for two reasons. First, our definition must apply across fishes even to clades that show only subtle dichromatism. Second, we do not always know which cases of dichromatism are unimportant for mate choice, as most fishes have not been studied behaviorally (Amundsen 2003).

We coded sexual dichromatism as present in a species if at least one source described sex differences in color (table A2). There were two ways that species could be coded as monochromatic (table A2). The first way was if a source stated that the species (or higher taxon to which it belonged) was monochromatic. However, we anticipated that many sources were unlikely to explicitly state that a species was monomorphic if the authors' goal was species identification (as for field guides). Therefore, we also coded species as monochromatic if the species' color in life was described but no sex differences were mentioned. The benefit of including these species is the increased power to detect variation in diversification rates (Davis et al. 2013). Our literature search supported our supposition that dichromatism is likely to be reported if it exists, but authors explicitly report monochromatism less often (text A2; table A3). Nevertheless, we performed analyses without these species and obtained similar results (see below; table A4).

Phylogenetic Framework

We used a time-calibrated maximum likelihood phylogeny (Rabosky et al. 2018) of ray-finned fishes including 11,638 species with DNA sequence data (36.9% of all described species). We included only species with sequence data because semirandom grafting of unsampled species is inappropriate for analyzing trait evolution at the species level (Rabosky 2015). We removed duplicate and unidentified species as well as species for which we could not find information on sexual dichromatism from the literature (see "Results"). Species sampling among orders in this reduced phylogeny (10,898 species) was correlated with their described richness ($n = 68$ orders; $r = 0.97$; $P < .001$; text A1).

We initially performed analyses at three phylogenetic scales: (1) across all ray-finned fishes, (2) within each of 18 clades individually, and (3) within eight selected subclades of the six largest of those 18 clades. Details for all 18 clades and eight subclades are given in table A5. To delimit clades in all cases, we targeted monophyletic higher taxa (families and orders) in which both monochromatism and dichromatism were present in ≥10% of the species. State-dependent speciation and extinction (SSE) methods can give problematic results when one state is rarer than 10% (Davis et al. 2013). To maximize species sampling, we used orders instead of families in cases where we could include additional species while maintaining this proportion. These 18 clades contained 93–1,098 species in the tree (mean = 349.2, SD = 265.4). The six largest clades (Characiformes, Cichlidae, Cyprinidae, Cyprinodontiformes, Gobiiformes, and Scorpaeniformes) included eight families and subfamilies that were also suitable for analyses under these criteria. These eight subclades included 111–438 species (mean = 273.8, SD = 123.8).

To assess how phylogenetic uncertainty may affect our results, we repeated hidden state speciation and extinction (HiSSE) analyses (see below) on three clades with alternative published phylogenies: Cichlidae (Burress and Tan 2017), Labridae (Siqueira et al. 2016), and Poeciliidae (Reznick et al. 2017). These clades were particularly important because of previous studies linking dichromatism and diversification within them (e.g., Kazancıoğlu et al. 2009; Wagner et al. 2012; Furness et al. 2019). Furthermore, species sampling in these trees was similar to that in the main tree (Rabosky et al. 2018). Thus, any differences in results should be related to the trees (topology and divergence times) and not sampling. Details of these alternative trees are in text A3 and table A6.

We also used a rank-free approach to select clades (Poe et al. 2020). To test whether temporal scale influences our results, we sliced the phylogeny at different time points. We collected all subtrees produced by slicing the tree at 100, 80, 60, and 40 million years (myr) ago, respectively. Slicing was performed using the chainsaw2 function in BioGeoBEARS version 1.1.2 (Matzke 2014). We then filtered the resulting clades to find those suitable for SSE analyses (>100 species, both states present in ≥10% of species). This yielded 12 clades ~100 myr in age, 16 at ~80 myr, 15 at ~60 myr, and six at ~40 myr, for a total of 49 clades. For a given slice, most clades were subsets of those from older slices. Details of rank-free clades are in tables A7–A10.

Diversification Analyses

We primarily tested for associations between sexual dichromatism and diversification using the HiSSE framework implemented in the R package hisse version 1.9.0 (Beaulieu and O'Meara 2016). The HiSSE framework is an advance over previous SSE methods because it can detect rate shifts that are not caused by the trait of interest. It can thereby reduce false associations between diversification rates and the focal trait (Rabosky and Goldberg 2015). We performed identical HiSSE analyses on each of the 27 clades separately (all ray-finned fishes, 18 fish clades, and eight subclades) and the 49 clades from the rank-free approach. We compared the fit of 14 dichromatism-dependent models of diversification (in which dichromatism accounts for some or all of the diversification rate heterogeneity in the tree) to nine dichromatism-independent models (in which dichromatism is unrelated to diversification rate heterogeneity). We compared the fit of dichromatism-dependent models to dichromatism-independent models of similar complexity (Beaulieu and O'Meara 2016; Harrington and Reeder 2017). Details of the 23 models are given in table A11. To correct for incomplete species sampling, we calculated the proportion of unsampled species for each clade using rfishbase (Boettiger et al. 2012), assuming that this proportion was identical between monochromatic and dichromatic species. We did this because the total number of monochromatic and dichromatic species among ray-finned fishes is unknown. However, supplemental analyses suggest that monochromatic and dichromatic species have similar chances of being sampled in the phylogeny (text A1). Relative fit of models was determined using Akaike weights (AICw; Burnham and Anderson 2002).

When a dichromatism-dependent model of diversification had the best fit, a range of relationships between dichromatism and diversification were possible. Dichromatism could have positive or negative effects on speciation, extinction, and diversification. To characterize this relationship for each clade, we obtained model-averaged rates associated with each species, with the contribution of each model toward the mean proportional to that model's AICw (Caetano et al. 2018). Only models with ≥5% of the AICw of the model set were included in model averaging to avoid undue influence of poorly supported models (Caetano et al. 2018). Next, we tested whether model-averaged speciation, extinction, and net diversification rates were significantly different between monochromatic and dichromatic species, using phylogenetic ANOVA (Garland et al. 1993) implemented in phytools version 0.6-44 (Revell 2012). Note that in some cases, a dichromatism-independent model received 100% of the AICw but mean rates were still significantly different between monochromatic and dichromatic species using phylogenetic ANOVA. We interpret this result as indicating that other (hidden) factors are ultimately responsible for rate shifts (Beaulieu and O'Meara 2016). A recent study suggested that it can be mathematically difficult to separate the contributions of speciation and extinction to changes in diversification through time (Louca and Pennell 2020), but it is unclear whether this problem applies to SSE models because they are more complex than birth-death models.

At the scale of all ray-finned fishes, we also tested the robustness of our HiSSE results using Bayesian analysis of macroevolutionary mixtures (BAMM). BAMM (Rabosky 2014; Rabosky et al. 2014) is a Bayesian framework for detecting shifts in diversification. There are two relevant differences between this approach and HiSSE. First, BAMM estimates diversification rate shifts independently from trait evolution. Second, HiSSE is limited by the number of rate shifts (i.e., hidden states) it can model, while BAMM has no limit on potential rate shifts. We acknowledge that BAMM may still be relatively insensitive to rate variation, especially for small clades (Moore et al. 2016; Rabosky et al. 2017; Meyer and Wiens 2018). We used structured rate permutations on phylogenies (STRAPP; Rabosky and Huang 2016), which uses a permutation test to detect an association with a binary trait and diversification rate shifts estimated by BAMM. This approach is best applied only to very large phylogenies because many rate shifts are needed to gain enough power to detect associations with a trait (Rabosky and Huang 2016).

We processed the BAMM output performed by Rabosky et al. (2018) using BAMMtools version 2.1.6 (Rabosky et al. 2014). We generated a null distribution of the Mann-Whitney U-test statistic by performing 1,000 permutations of the BAMM rate shifts associated with each species, using the traitDependentBAMM function in BAMMtools. This null distribution was used to test for associations between dichromatism and rates of speciation, extinction, and diversification. We used alternative rates estimated using a time-constant and time-variable BAMM model. We also performed tests using only species with direct information about the presence or absence of dichromatism ($n = 8,613$ species).

Alternative Perspectives on Color

We tested the sensitivity of our results to (1) treating sexual dichromatism as a binary variable and (2) using human perceptions of color. These analyses are summarized here, with details in texts A4 and A5.

Darwin (1871) originally considered the degree of dimorphism to be a proxy for the strength of sexual selection. Therefore, even if sex differences are present, diversification rates may be elevated only when dichromatism is dramatic. To test this possibility, we used color data from the literature for two well-studied clades: Etheostomatinae (darters; Bossu and Near 2015) and Labridae (wrasses and parrotfishes; Hodge et al. 2020). These studies each quantified sexual dichromatism on a continuous scale using photographs of males and females of each species. We tested for a relationship between the degree of dichromatism and tip-associated speciation rates from BAMM (calculated by Rabosky et al. 2018) using phylogenetic generalized least squares (Freckleton et al. 2002). This relationship was not significant in either clade (table A12). High speciation rates were found along the continuum from monochromatic to extremely dichromatic species (fig. A1; figs. A1–A6 are available online). These results were consistent with those using binary state models for these two clades (see "Results"; text A4).

Like many previous studies (e.g., Wagner et al. 2012), our data set was based on human perceptions of fish color. Many birds that appear sexually monochromatic to humans are actually dichromatic in the ultraviolet (UV) spectrum (Eaton 2005). We are not aware of any studies in fishes that found that a species that was sexually dichromatic in the UV spectrum appeared monochromatic to humans, as is the case for birds (Eaton 2005; but see Siebeck et al. 2010 on UV patterns and species discrimination in fishes). Furthermore, many fishes that are capable of UV vision lack body coloration visible in UV (Siebeck and Marshall 2001). Fishes may use UV vision in many contexts, such as feeding (Losey et al. 1999). Thus, UV vision in fishes need not be relevant to sexual selection.

Nevertheless, we assessed how our results would be affected by relying on human color perception to code the presence of dichromatism (text A5). We used a compendium of λ_{max} (peak sensitivity wavelength of photoreceptors) estimates across 277 species of ray-finned fishes (Schweikert et al. 2018) to identify fishes with UV-sensitive vision. First, we found that fishes with UV vision were significantly more likely to appear sexually dichromatic to humans than other fishes (χ^2 test: $\chi^2 = 5.97$, $P = .0145$, $n = 237$ species). This suggests that fishes with the greatest potential to see colors in UV are also likely to have dichromatic coloration detectable by humans. Second, we tested whether speciation rates were significantly different among monochromatic and dichromatic fishes, assuming an extreme case in which all fishes with UV vision are sexually dichromatic even if they were assigned as monochromatic based on human color. We found that any differences in speciation rates associated with dichromatism were driven by biased sampling of dichromatic cichlids in the vision data set. Once cichlids were removed, there were no differences in speciation rates between monochromatic and dichromatic species, regardless of whether we recoded species with UV vision as dichromatic (table A13). Overall, we found no evidence that our results across fishes would be overturned by the failure to observe sexual dichromatism outside the human visible spectrum.

Results

Prevalence of Sexual Dichromatism

We obtained information from the literature on the presence and absence of sexual dichromatism for 10,898 species of ray-finned fishes, including most (93.6%) of the species sampled in the phylogeny (Rabosky et al. 2018) and 34.6% of all described species. Data were obtained from 196 sources (data set S1, deposited in the Dryad Digital Repository [https://doi.org/10.5061/dryad.hqbzkh1bs; Miller et al. 2021]), including primary literature, online databases, field guides, taxonomic compilations, aquarist resources, and expert opinion (for two families with limited information). There was a mean of 2.5 sources associated with each species (SD ± 1.7, range = 1–15).

Sexual dichromatism was reported in 3,154 sampled species (28.9% of species in our data set). This proportion is not significantly different from an earlier estimate of 27.0% (Mank 2007; χ^2 test: $\chi^2 = 1.45$, $P = .23$; text A1). This implies that the prevalence of sexual dichromatism would not change greatly with additional sampling. There was no correlation between the proportion of species sampled in the phylogeny for each order and the proportion of dichromatic species in that order ($n = 68$ orders; $r = 0.17$; $P = .16$; text A1). Thus, sexual dichromatism did not appear to influence species sampling in this phylogeny.

Diversification Rates across All Ray-Finned Fishes

Our results show that sexual dichromatism does not significantly impact diversification rates when all ray-finned fishes are included (fig. 1). Using HiSSE, a dichromatism-independent model received 100% of the AICw (table A14). Using phylogenetic ANOVA on model-averaged rates (table A15), we found no significant difference in speciation rates between monochromatic and dichromatic species (mean $\lambda_{monochromatic} = 0.197$ lineages per myr [0.058–0.227; first and third quantile]; $\lambda_{dichromatic} = 0.241$ [0.070–0.310]; $P = .491$). We also found no significant difference in extinction rates ($\mu_{monochromatic} = 0.123$ [0.007–0.128]; $\mu_{dichromatic} = 0.159$ [0.012–0.205]; $P = .497$) or net diversification rates ($r_{monochromatic} = 0.074$ [0.051–0.097]; $r_{dichromatic} = 0.081$ [0.058–0.105]; $P = .273$). Although SSE methods have the power to detect trait-dependent diversification in clades with only a few hundred species (Davis et al. 2013), we did not find such an association with 10,898 species.

Using STRAPP, we also found no significant differences between monochromatic and dichromatic species in rates of speciation ($P = .53$ under a BAMM time-variable model, $n = 10,898$ species), extinction ($P = .61$), or net diversification ($P = .53$), regardless of the BAMM model used (table A4). We also performed STRAPP analyses that excluded the 2,285 species that were coded as monochromatic based solely on color descriptions that did not mention differences between the sexes. Again, we found no differences in rates (table A4).

Patterns within Individual Clades

We first fit HiSSE models on 18 clades individually. For illustrative purposes, we compared the summed AICw of 14 dichromatism-dependent models with the summed AICw for nine dichromatism-independent models (table A11). Scores of individual models are given in table A14, and model-averaged rates are given in table A15. Dichromatism-dependent models of diversification received >80% of the AICw in only four clades (figs. 2, A2; table A14). In Tetraodontiformes (pufferfishes and relatives), dichromatic species had higher speciation rates but also higher extinction rates, such that monochromatic species had higher net diversification rates. Centrarchiformes (sunfishes and relatives) showed no significant difference in speciation or diversification rates. However, extinction rates were significantly lower in dichromatic species. Anabantiformes (bettas and relatives) and Blenniiformes (blennies) had significantly positive relationships between dichromatism and net diversification. However, in Anabantiformes, the difference in diversification rates was again due to lower extinction rates in dichromatic species, not faster speciation rates.

Among the remaining 14 clades, seven showed no evidence for an effect of dichromatism on diversification (figs. 2, A3). The other seven clades had only equivocal evidence for a positive relationship (three clades; fig. A4) or a negative relationship (four clades; fig. A5). These seven equivocal cases occurred when dichromatism-dependent and dichromatism-independent models received similar support (e.g., Gobiiformes and Percidae; AICw of dichromatism-independent models = 40% and 58%, respectively) or when a dichromatism-independent model had strong fit but mean rates were still significantly different using phylogenetic ANOVA (table A15). This latter pattern implies that diversification is associated with other (hidden) factors that partially overlap with dichromatism (Beaulieu and O'Meara 2016).

Surprisingly, the 14 clades in which dichromatism-dependent models received equivocal or no support encompassed many classic model systems that linked sexual dichromatism to reproductive isolation and/or speciation. These clades included Cichlidae (sum of AICw of dichromatism-independent models = 100%; n = 720 species), Cyprinodontiformes (guppies and relatives; AICw = 100%; n = 572), Labridae (wrasses and parrotfishes; AICw = 100%; n = 337), and Percidae (darters; AICw = 58%; n = 218). We found similar results when using alternative phylogenies of Cichlidae and Labridae (tables A16, A17).

Patterns at Shallower Phylogenetic Scales

Among the 18 clades, the six largest were Characiformes, Cichlidae, Cyprinidae, Cyprinodontiformes, Gobiiformes, and Scorpaeniformes. Dichromatism-independent models received 100% of the AICw in five of these six clades (fig. 2; table A14). However, support for dichromatism-dependent models strongly increased in four of eight subclades, relative to the larger clade to which they belonged (to 39% of the AICw in Characidae, 65% in Poeciliidae, 86% in Leuciscinae, and 100% in Gobiidae; fig. 3; table A18). The relationships between dichromatism and diversification were variable among these groups. Characidae (tetras) and Leuciscinae (minnows) had higher net diversification rates in monochromatic species (table A19; fig. A6). Dichromatic gobies (Gobiidae) had higher speciation rates but also higher extinction rates, leaving no significant difference in net diversification rates. In Poeciliidae, higher net diversification rates associated with dichromatism were due to lower extinction rates, not higher speciation rates (table A19; fig. A6). We also recovered a positive effect of dichromatism on net diversification using an alternative phylogeny of Poeciliidae (Reznick et al. 2017). This effect was due to both speciation and extinction rates using this tree (tables A16, A17). We found no evidence for higher diversification rates associated with dichromatism in the subfamilies Pseudocrenila brinae (African cichlids) and Cichlinae (Neotropical cichlids; fig. 3; table A18; fig. A6), mirroring the results for Cichlidae as a whole (fig. 2). This surprising result is robust to use of an alternative cichlid phylogeny (Burress and Tan 2017; tables A16, A17).

Rank-Free Time Slice Approach

HiSSE results among 49 clades selected using time slices (fig. 4*A*; tables A7–A10) showed patterns similar to results from ranked clades. Only one of the 12 oldest clades (100-myr slice) had strong support for any effect of sexual dichromatism on diversification (fig. 4*B*; table A20). In this clade (loaches), the summed AICw of dichromatism-dependent models was 85%, and dichromatism had a negative effect on net diversification (table A21). The corresponding weight for the remaining 11 clades ranged from 0% to 41% and was <5% for eight clades (table A20).

Support for dichromatism-dependent models was higher among the clades from the 80-, 60-, or 40-myr time slices (fig. 4*B*; tables A22–A27). Most of these clades were nested within the 12 oldest clades from the 100-myr slice (tables A7–A10). Among these 12 clades, eight contained subclades with stronger support for dichromatism-dependent models than the clade as a whole (fig. 4*B*). For example, cichlids finally showed the expected support for dichromatism-dependent diversification at the youngest level. Subclades within the African and Neotropical cichlid lineages from the 40-myr slice each had strong support for dichromatism-dependent models (100% and 91% of the AICw, respectively; table A26), with a positive effect of dichromatism on net diversification (fig. 4*B*; table A27). Among all clades with strong support for dichromatism-dependent models, there was no common tendency for dichromatism to increase or decrease speciation, extinction, or net diversification.

Support for dichromatism-dependent HiSSE models did not linearly increase with decreasing crown-group age (fig. 4*C*). The 100-myr subset of clades collectively had poor

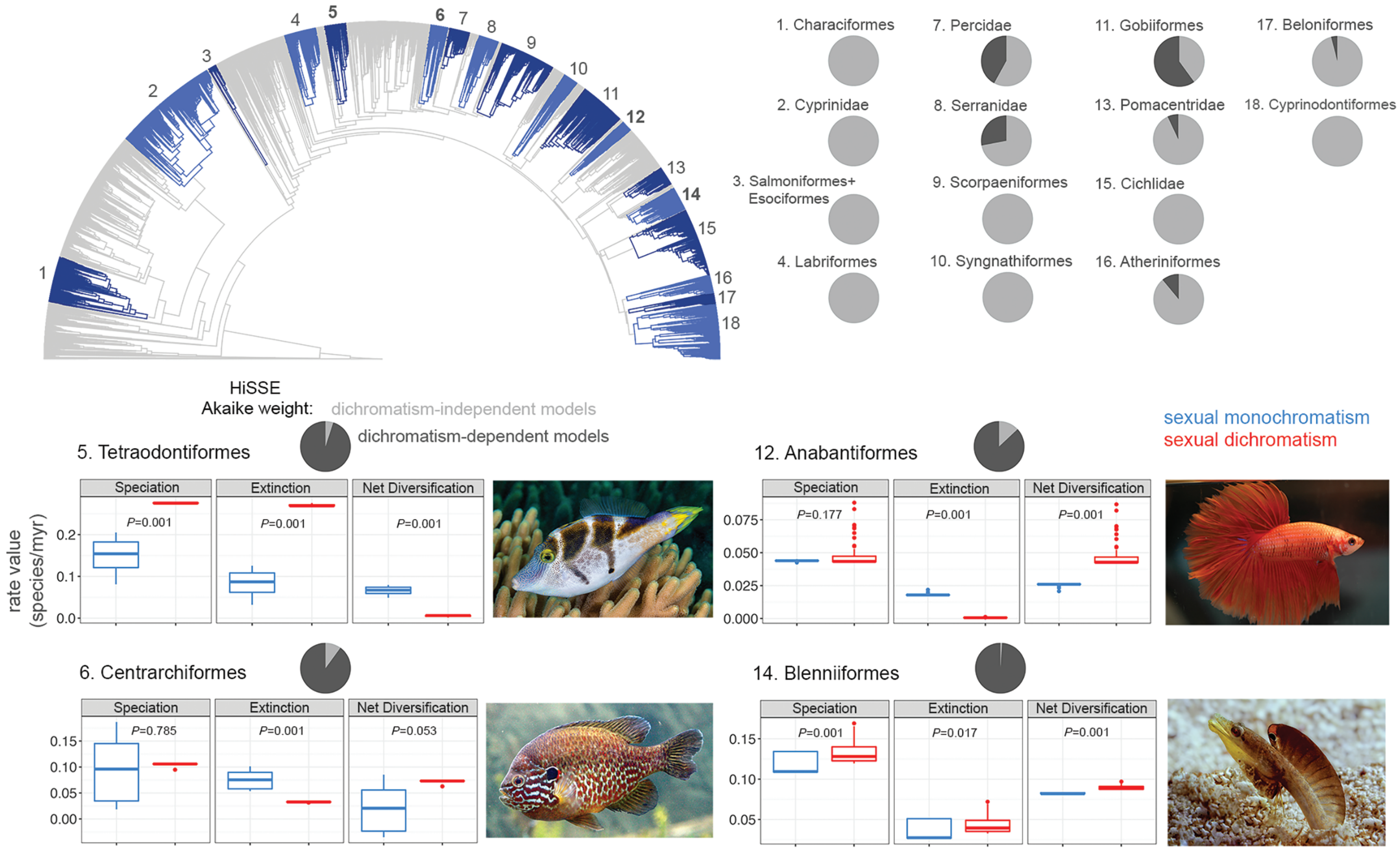


Figure 2: Sexual dichromatism and diversification within 18 fish clades. Clades chosen for analyses (table A5) are highlighted on the phylogeny in alternating shades of blue for visibility. Pie diagrams indicate the relative Akaike weights (AICw) for 14 dichromatism-dependent hidden state speciation and extinction models (dark gray) versus nine dichromatism-independent models (light gray). Dichromatism-dependent models of diversification received >80% of the AICw support in four of 18 clades (*bottom*). Boxplots show model-averaged rates for individual species, including medians, first and third quartiles, and outliers (outside the 95% confidence interval). Rates for monochromatic species are shown in boxplots on the left in blue; rates for dichromatic species are shown on the right in red. Model fits are given in table A14. Model-averaged rates for all clades are given in table A15 and figs. A2–A5. Photograph credits: Tetraodontiformes: François Libert; Centrarchiformes: Wikimedia user Cephas, CC BY-SA 3.0; Anabantiformes: Flickr user Daniella Vereeken, CC BY 2.0; Blenniiformes: Betty Wills (Atsme), Wikimedia Commons, CC-BY-SA 4.0.

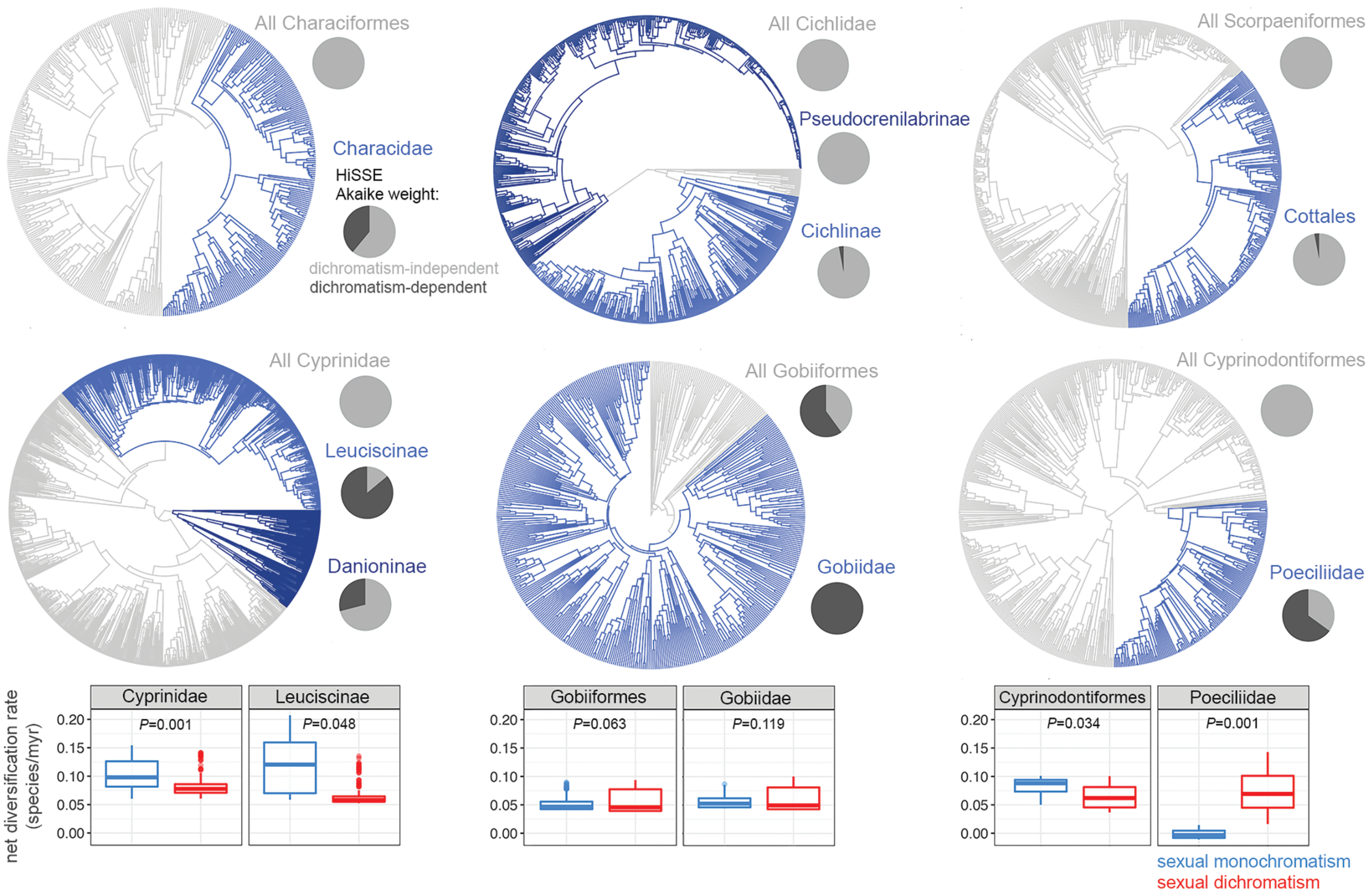


Figure 3: Sexual dichromatism and diversification at shallower phylogenetic scales (six subclades from the largest of the 18 clades in fig. 2). Pie diagrams indicate relative Akaike weights for 14 dichromatism-dependent hidden state speciation and extinction models (dark gray) versus nine dichromatism-independent models (light gray). The bottom row shows differences in rates between three subclades and their larger clades for those subclades for which dichromatism-dependent models received the most support. Boxplots show model-averaged net diversification rates for individual species, including medians, first and third quartiles, and outliers (outside the 95% confidence interval). Rates for monochromatic species are shown in boxplots on the left in blue; rates for dichromatic species are shown on the right in red. Model fits are given in table A18. Model-averaged rates of speciation, extinction, and net diversification are given for all subclades in table A19 and fig. A6.

support for an effect of dichromatism, but there was similar support among the 40-, 60-, and 80-myr subsets. There was no correlation between model support and the proportion of species sampled or the proportion of species with sexual dichromatism (table A28). Instead, model support was negatively correlated with clade size (fig. 4*C*). This pattern appeared when we pooled all 49 clades for comparison (clade size: Spearman's $\rho = -0.680$, $P < .001$; clade age: $\rho = -0.264$, $P = .073$) and also within the 100-, 80-, and 60-myr subsets individually (table A28).

Among all rank-free clades, the largest clade with support for dichromatism-dependent diversification contained 1,107 described species (summed AICw = 72%). None of the 13 clades larger than this (1,442–4,139 species) had a summed AICw >5% for dichromatism-dependent models. Eleven clades had strong support for dichromatism-dependent models (AICw >80%). These clades ranged from 39.5 to 93.3 myr old (mean = 62.5) and had 106–414 sampled tips (mean = 202.3) and 144–1,041 described species (mean = 556.6). Clades with equivocal support (AICw = 40%–70%) tended to be small (<200 tips, 167–339 described species). Putting these observations together, the power to detect dichromatism-dependent diversification was sufficient in clades with >300 species, yet it was unlikely to be detected in clades with >1,000 species.

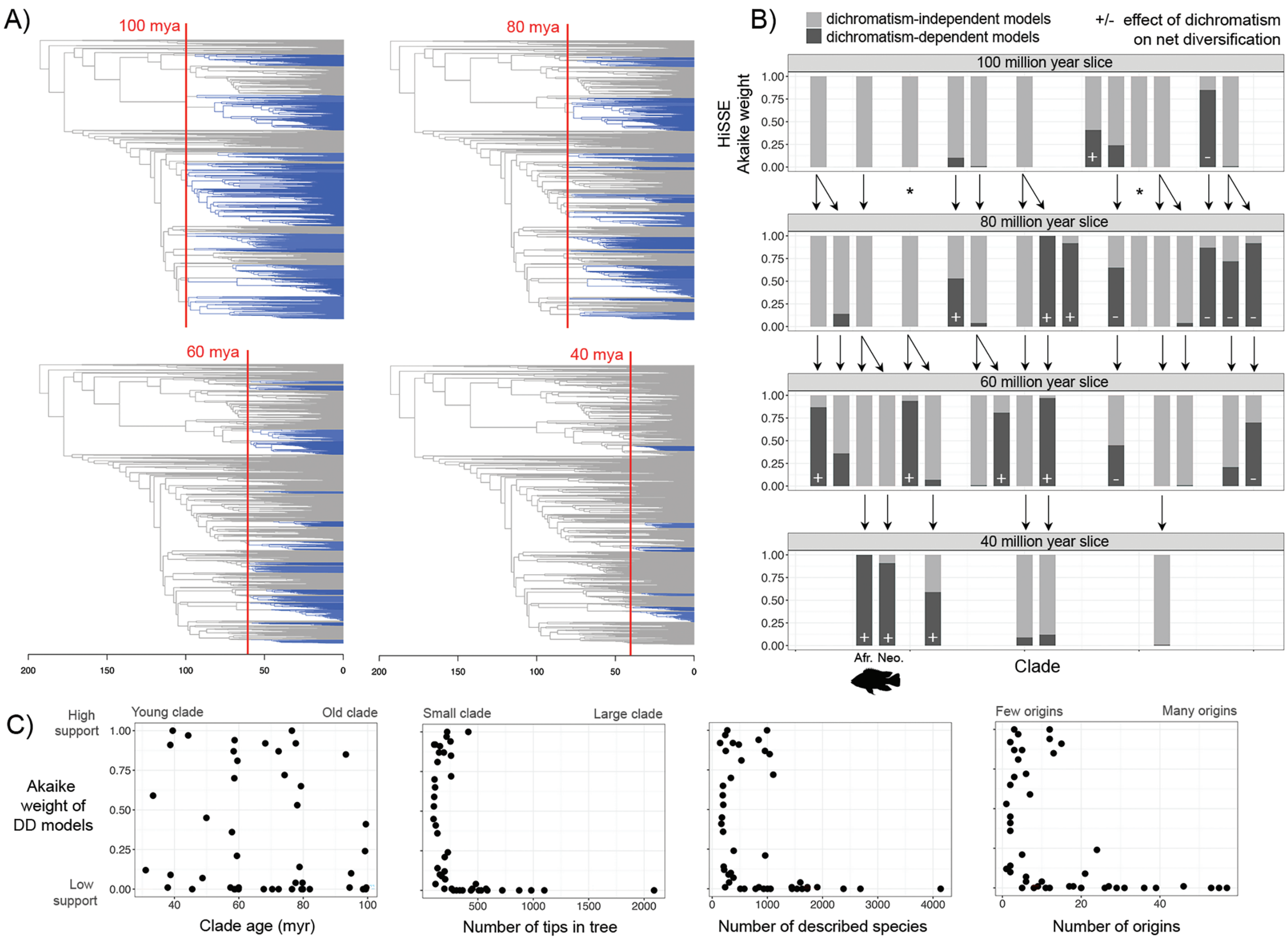
We also considered whether the number of independent origins of monochromatism or dichromatism in a clade was related to the support for dichromatism-dependent models, as expected if the power to detect this effect increases with greater phylogenetic replication. For each clade, we counted the number of transitions to either state using ancestral-state reconstructions from the best-fitting HiSSE model and used the smaller of the two counts in correlations with model support. This relationship was negative, the opposite of our prediction ($\rho = -0.612$, $P < .001$; table A28). The number of origins was strongly correlated with the size of the phylogeny ($\rho = 0.804$, $P < .001$). These results further suggest that clade size is the most consistent predictor of support for dichromatism-dependent HiSSE models.

Discussion

A major goal in evolutionary biology is to identify the traits that influence diversification rate differences among clades (Wiens 2017). Since Darwin (1871), sexual dichromatism has been thought to be related to speciation and thereby to faster rates of net diversification (speciation minus extinction) and greater species richness (Lande 1981; West-Eberhard 1983; Ritchie 2007; Kraaijeveld et al. 2011; Boughman 2014). Classic studies in several fish families have provided strong evidence that sexual dichromatism is related to assortative mating (Houde and Endler 1990; Seehausen et al. 1997; Elmer et al. 2009), reproductive isolation (Boughman 2001; Mendelson 2003; Seehausen et al. 2008), and diversification (Kazancıoğlu et al. 2009; Wagner et al. 2012; Smith et al. 2015; Furness et al. 2019; McGee et al. 2020). We assembled and analyzed a data set of unprecedented size to address how dichromatism impacts diversification rates across ray-finned fishes. Large data sets can reduce potential biases caused when well-studied groups are not broadly representative of all taxa (Beaulieu and O'Meara 2018). In addition, large data sets allowed us to test for scale dependency in the effects of dichromatism on diversification rates. Researchers now recognize that the factors that drive diversification may differ depending on the temporal or taxonomic scale examined (Jablonski and Bottjer 1991; Benton 2009; Kraaijeveld et al. 2011; Bellwood et al. 2017; Graham et al. 2018). Yet empirical demonstrations of scale-dependent effects of traits on diversification are rare (but see Huang and Rabosky 2014; Harrington and Reeder 2017; Hernández-Hernández and Wiens 2020).

Our results suggest that sexual dichromatism can explain diversification rate differences but only over limited phylogenetic scales. For example, we found evidence that dichromatism increases net diversification in the family Poeciliidae (fig. 3). However, we found no such relationship in the order Cyprinodontiformes, which contains Poeciliidae (fig. 3). Similarly, it is well established that nuptial colors help to maintain reproductive isolation among closely related cichlid species (Seehausen et al. 1997, 2008; Elmer et al. 2009), and sexual dichromatism can help explain which cichlid lineages have radiated in African lakes (Wagner et al. 2012; McGee et al. 2020). However, we found no support for dichromatism-dependent HiSSE models for Cichlidae or for its two major subfamilies (fig. 3). We eventually found strong support for a positive relationship between dichromatism and diversification in clades within each subfamily that were selected using a rank-free time cut-off of 40 million years (fig. 4*B*).

The scale-dependent effect of sexual dichromatism on diversification rates has been previously suggested. Kraaijeveld et al. (2011) compared different studies of birds and suggested that sexual dichromatism has the strongest effect at shallow scales (e.g., within species or genera; but see Cooney et al. 2017). They attributed this pattern to the extinction of newly formed species over time, eroding the signal of diversification driven by sexual selection. This mechanism should homogenize diversification rates and reduce rate disparities among older clades. However, our results suggest an additional cause for the scale-dependent effect (even if extinction is present). Specifically, the disparity in rates among fish clades was often greater than diversification rate variation within clades (e.g., rates among the 18 clades in figs. 2, A2). For example, even monochromatic cichlids have higher diversification rates than dichromatic


A)
100 mya
80 mya
60 mya
40 mya
200
150
100
50
0
B)
dichromatism-independent models
dichromatism-dependent models
+/- effect of dichromatism on net diversification
HiSSE Akaike weight
100 million year slice
80 million year slice
60 million year slice
40 million year slice
1.00
0.75
0.50
0.25
0.00
+
-
*
Afr. Neo.
Clade
C)
High support
Low support
Akaike weight of DD models
Young clade
Old clade
Clade age (myr)
40
60
80
100
Small clade
Large clade
Number of tips in tree
500
1000
1500
2000
Number of described species
0
1000
2000
3000
4000
Few origins
Many origins
Number of origins
0
20
40

anabantiforms (fig. A2). Our rank-free comparisons also shed light on the cause of the scale-dependent effect. Support for dichromatism-dependent HiSSE models was negatively correlated with clade size, regardless of clade age (fig. 4*C*; table A27). The support for dichromatism-independent models for larger clades (figs. 2–4) indicates that other factors (hidden states) better explain diversification rate variation among subclades.

On the basis of these observations, we suggest that large clades are likely to be heterogeneous in other variables that drive diversification, and these variables could have stronger influence on diversification rates than sexual dichromatism. For example, habitat and trophic divergence are thought to precede divergence in sexual signals in vertebrate radiations (Mesnick 1996; Streelman and Danley 2003; Bellwood et al. 2017). These ecological factors may drive diversification rate differences among distantly related clades. Sexual dichromatism may then act on these background rates within clades. This top-down explanation is distinct from the bottom-up explanation (erosion of signal through time) of past studies (e.g., Kraaijeveld et al. 2011).

Many factors influence diversification rates across a large clade like actinopterygian fishes. Some readers may be concerned that no signal of any single trait on diversification rates could appear at this large scale because of confounding factors influencing diversification. However, several recent studies have shown significant effects of individual traits on speciation or net diversification rates across distantly related actinopterygian clades using similar data and methods as in this study. These traits include latitude (using HiSSE: Miller et al. 2018; using BAMM: Rabosky et al. 2018), diet (Siqueira et al. 2020), lacustrine habitat (Miller 2021), diadromy (Corush 2019), and several other variables (Tedesco et al. 2017). In addition, single traits (e.g., microhabitat) have been shown to have significant explanatory power at much deeper scales, including across all vertebrates (Wiens 2015) and all animals overall (Jezkova and Wiens 2017).

Why might some traits matter more than others over deep time? It may be that traits must have a consistent and replicated effect among clades for this effect to appear in whole-clade analyses. For example, not only are high latitudes positively related to diversification rates in marine fishes, but also this positive effect appears independently in distantly related clades found near both the northern and the southern poles (Rabosky et al. 2018). In contrast, sexual dichromatism does not have an effect on diversification in all clades where it is present (even among young clades; figs. 3, 4). When it does, the effect can be positive or negative (figs. 2–4). Thus, there is no apparent effect when these clades are combined (fig. 1; table A4).

Our results have methodological implications for diversification rate studies. Analyses of very large clades are becoming increasingly common (e.g., Huang and Rabosky 2014; Miller et al. 2018; Rabosky et al. 2018; Hernández-Hernández and Wiens 2020). Greater sampling affords greater power to detect trait-dependent diversification (Davis et al. 2013) and uncover generalities beyond model clades (Beaulieu and O'Meara 2018). However, the strongest support for an effect of sexual dichromatism was found among clades with only ~200 tips (fig. 4*C*). This conflict may be relevant to other trait-dependent diversification studies. Counterintuitively, simply performing analyses on the largest possible phylogeny may improve power but lead to an incorrect conclusion that the trait is entirely irrelevant to diversification. We are not aware of existing comparative methods that can automatically detect the scale at which a trait is important for diversification. Therefore, we encourage researchers studying large clades to also perform analyses on a range of subclades.

Our results suggest that the presence of sexual dichromatism may not be enough to influence diversification rates by itself. There are several potential reasons for this. First, sexual dichromatism may promote speciation only when certain extrinsic and intrinsic conditions are met, such as environments with high water clarity (Seehausen et al. 1997, 2008; Hodge et al. 2020) or when male courtship or ornaments are also present (Furness et al. 2019). Second, some authors have suggested that the rate of change in sexual signals is what drives diversification (Gomes et al. 2016). Given this idea, we may not expect higher diversification rates in groups with sexual signals that

Figure 4: Sexual dichromatism and diversification with time. *A*, Summary of our rank-free clade selection procedure. We sliced the ray-finned fish phylogeny at 100, 80, 60, and 40 myr ago and collected the resulting subclades. Subclades that were suitable for hidden state speciation and extinction (HiSSE) analyses are highlighted in blue. Clade identities are given in tables A7–A10. *B*, Results of HiSSE analyses on rank-free clades. Bars show the relative Akaike weights for 14 dichromatism-dependent models (dark gray) versus nine dichromatism-independent models (light gray). Each bar represents one clade in *A*. Signs indicate whether sexual dichromatism has a positive (+) or negative (−) effect on net diversification. Full HiSSE results are given in tables A20–A27. Clades are positioned vertically such that nested subclades are below their parent clade, indicated with arrows. Some clades have more than one nested subclade (double arrows). An asterisk indicates that an identical clade was produced with the 80-myr slice as with the 100-myr slice because of the stem branch crossing both time slices. Fish icon denotes African and Neotropical cichlid clades (image from Phylopic, with credit to Milton Tan). *C*, Comparing the support for dichromatism-dependent HiSSE models when all 47 unique clades are pooled. We found a hook-shaped relationship with support and clade size. We also found this relationship using the number of origins (smaller count of the origins of monochromatism or dichromatism). Full correlation results are given in table A28.

are present but relatively invariant among species. Third, diversification rates may be associated with only elaborate dichromatism, if the degree of dimorphism is a proxy for the strength of sexual selection (Darwin 1871). We did not find support for this hypothesis in wrasses or darters (text A4; table A12; fig. A1). However, we have not tested this hypothesis among all fish clades. The three scenarios listed above may explain why diversification rates vary among dichromatic species. However, these factors cannot explain why monochromatic species often had higher diversification rates than dichromatic species.

Why might sexually monochromatic fishes have diversification rates that are similar to (or faster) than those of dichromatic fishes? In some clades, the absence of sexual dichromatism may not indicate the absence of assortative mating or sexual selection. Monochromatic fishes may have other features involved in species recognition or mate choice. Hamlets (Serranidae) have the fastest diversification rates among reef fishes (Siqueira et al. 2020). Sympatric species of hamlets are reproductively isolated by species-specific but sexually monochromatic color patterns (Hench et al. 2019). Butterflyfishes are another sexually monochromatic clade in which species-specific patterns may maintain species boundaries (Hemingson et al. 2019). Diversification rates among shallow marine fishes might be better explained by color in general rather than sexually dimorphic colors (Mesnick 1996; Bellwood et al. 2017). In environments with poor color transmission, signals that are bioluminescent, acoustic, tactile, and electrical are often involved in courtship and may also increase diversification rates (Mesnick 1996; Davis et al. 2014). In fact, these signals could have an even stronger and more consistent effect on diversification than color. Mesnick (1996) found that nonvisual sexual signals were associated with faster diversification in all fish clades with these signals. In contrast, visual signals had positive, negative, or no effect on diversification. The possibility remains that sexual selection in general will help explain variation in diversification rates among ray-finned fishes but only when all sexually selected signals are considered (Mesnick 1996).

Observations within fishes (e.g., assortative mating among populations) imply that dichromatism increases species richness by increasing speciation rates, as predicted by classic literature (Darwin 1871; Lande 1981; West-Eberhard 1983). Yet higher diversification rates in dichromatic lineages were due to lower extinction rates (not faster speciation rates) in several clades, including Anabantiformes, Centrarchiformes, and Poeciliidae (fig. 2; tables A14, A18). In some clades, dichromatism also decreased speciation (e.g., Leuciscinae) and increased extinction (e.g., Blenniiformes, Tetraodontiformes). There are several mechanisms that might explain these disparate effects. Sexual selection can increase extinction risk if sexually selected traits increase mortality (Promislow et al. 1992) but can also reduce extinction by facilitating the purging of harmful mutations (Lumley et al. 2015). The effect of sexual selection on extinction in individual clades could depend on factors such as fecundity, population size, environmental stochasticity, and predation pressure (Promislow et al. 1992; Martínez-Ruiz and Knell 2017). Incorporating approaches from community ecology with diversification rate analyses may reveal the biological mechanisms for how sexual dichromatism influences speciation or extinction within clades (Tsuji and Fukami 2020).

Finally, what do the fish clades in which sexual dichromatism affects diversification have in common that is not shared by similarly sized clades in which dichromatism has no effect? Summarizing among all analyses (including ranked and rank-free clades), we found 13 independent clades with support for dichromatism-dependent HiSSE models (with either positive or negative effects) once the appropriate phylogenetic scale was determined. These clades were Anabantiformes, Blenniiformes, Centrarchiformes, two clades in Characiformes, two clades in Cichlidae, Gobiidae, Leuciscinae, Percidae, Poeciliidae, Tetraodontiformes, and a clade containing loaches. There were eight clades where dichromatism-dependent models were not supported even at smaller scales. These clades were Atheriniformes, Beloniformes, Labridae, Pomacentridae, Salmoniformes + Esociformes, Scorpaeniformes, Serranidae, and Syngnathiformes. Informal comparisons suggest two general differences between these groups (though there are exceptions). The first set of clades (with dichromatism-dependent diversification) are mostly freshwater, whereas the second set (dichromatism independent) are mostly marine. In addition, the first set of clades tend to show parental care (usually by males), whereas the second set generally lack parental care (Breder and Rosen 1966; Thresher 1984; Winemiller 1992). The codistribution of sexual dichromatism and parental care (Mank et al. 2005) could indicate stronger sexual selection than dichromatism alone if parental care is also under sexual selection (Alonzo 2012). Parental care may evolve in freshwater more often than in the ocean if pelagic eggs are adaptive in marine environments (Winemiller 1992). Further, gene flow from highly dispersive larvae may offset deme formation due to sexual selection on divergent male colors in marine species. Our data set on the presence of sexual dichromatism among fishes could be used to test these hypotheses in future comparative studies.

Conclusions

Researchers have found two patterns that potentially link sexual selection and speciation (Boughman 2014). The first is that premating isolation among many populations and species is based on differences in secondary sexual characteristics, such as nuptial coloration (Seehausen et al. 1997; Boughman 2001; Mendelson 2003; Elmer et al. 2009). The second pattern is a positive relationship between sexual dimorphism and diversification rates detected using comparative methods (Barraclough et al. 1995; Mesnick 1996; Mank 2007; Wagner et al. 2012; Furness et al. 2019). Our study suggests that the first pattern may not always lead to the second. On the basis of our results, the well-demonstrated effects of sexual dichromatism on speciation do not scale up to explain diversification rate variation across major clades (e.g., when comparing rates among monomorphic and dimorphic families and orders). Thus, our study helps resolve the paradox of the strong support for the effect of sexual selection on speciation from experimental and theoretical studies and the mixed support for this effect from macroevolutionary studies (Kraaijeveld et al. 2011; Tsuji and Fukami 2020).

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Statement of Authorship

E.C.M. conceptualized the work, led the data collection, designed and performed the analyses, and wrote the original manuscript. S.L.M. contributed to data collection. All authors helped to interpret the results and revise the manuscript.

Data and Code Availability

The complete dichromatism data set is included as data set S1. That data set as well as scripts needed to replicate analyses are deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.hqbzkh1bs; Miller et al. 2021).

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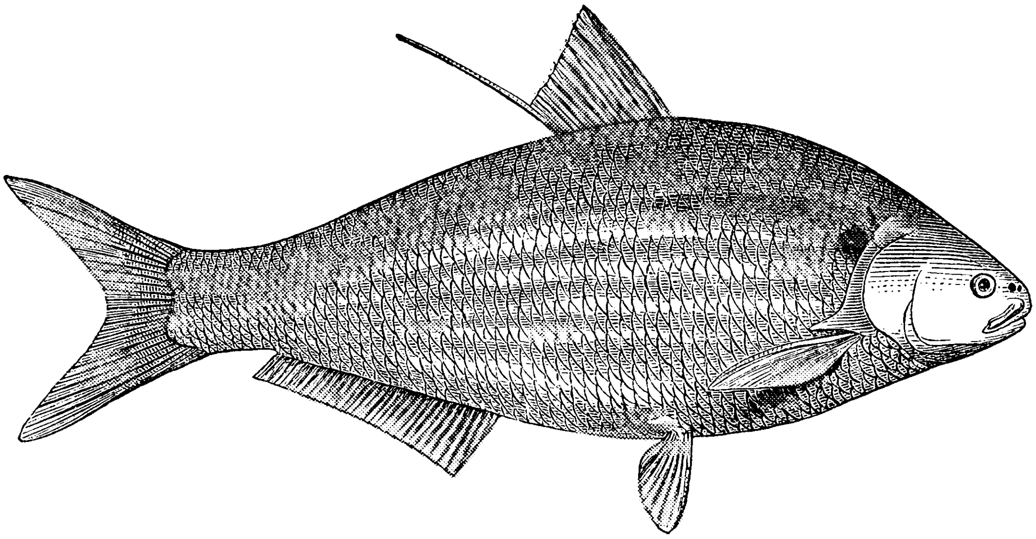

"Gizzard Shad (*Dorosoma Cepedianum*). We gave a short notice of this species in the 'Geology of New Jersey,' page 822, which we will quote and speak of more particularly. 'Occasionally the "gizzard shad" is carried by a freshet into inland streams usually having very small outlets, and thus imprisoned they thrive very well. A pond near Trenton was, in 1857, stocked with them, and is now full of specimens, some weighing five pounds apiece.' Besides this pond spoken of we know of one or two creeks that are annually visited by a few of these herring, and have occasionally seen *several bushels* hauled from the deep holes in the creeks they had entered." From "Notes on Fresh-Water Fishes of New Jersey" by Charles C. Abbott (*The American Naturalist*, 1870, 4:99–117).