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Phylogenetic perspectives on reef fish functional traits

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ABSTRACT

Functional traits have been fundamental to the evolution and diversification of entire fish lineages on coral reefs. Yet their relationship with the processes promoting speciation, extinction and the filtering of local species pools remains unclear. We review the current literature exploring the evolution of diet, body size, water column use and geographic range size in reef-associated fishes. Using published and new data, we mapped functional traits on to published phylogenetic trees to uncover evolutionary patterns that have led to the current functional diversity of fishes on coral reefs. When examining reconstructed patterns for diet and feeding mode, we found examples of independent transitions to planktivory across different reef fish families. Such transitions and associated morphological alterations may represent cases in which ecological opportunity for the exploitation of different resources drives speciation and adaptation. In terms of body size, reconstructions showed that both large and small sizes appear multiple times within clades of mid-sized fishes and that extreme body sizes have arisen mostly in the last 10 million years (Myr). The reconstruction of range size revealed many cases of disparate range sizes among sister species. Such range size disparity highlights potential vicariant processes through isolation in peripheral locations. When accounting for peripheral speciation processes in sister pairs, we found a significant relationship between labrid range size and lineage age. The diversity and evolution of traits within lineages is influenced by trait–environment interactions as well as by species and trait–trait interactions, where the presence of a given trait may trigger the development of related traits or behaviours. Our effort to assess the evolution of functional diversity across reef fish clades adds to the burgeoning research focusing on the evolutionary and ecological roles of functional traits. We argue that the combination of a phylogenetic and a functional approach will improve the

41 understanding of the mechanisms of species assembly in extraordinarily rich coral reef
42 communities.
43
44 *Key words*: diversification, coral reef, evolution, body size, life-history traits,
45 planktivory, range size, reef fish ecology.
46
47 CONTENTS
63

64 **I. INTRODUCTION**

65 Traits can be defined as any morphological, physiological, or phenological feature

66 usually measurable at the individual level of a species. Such features arise in lineages

67 through evolutionary time, usually being shared by species that have a recent common

68 ancestry (Webb *et al*., 2002; Peres-Neto, 2004; Swenson *et al*., 2006; Kraft *et al*., 2007).

69 On an ecological timescale, traits can mediate species interactions, thus influencing the

70 distribution of organisms and the structure of local communities. The interactions

71 among species are trait-mediated and have the potential to affect evolutionary processes,

72 which in turn act upon species' ecological roles and the diversity of traits available in

73 the regional pool (Cavender-Bares *et al.*, 2009). In this way, species traits form a link

74 between phylogenetic history (evolution and evolutionary time) and ecological

75 processes.

76   Functional traits are defined as properties of an organism that influence their

77 ecological and evolutionary performances in nature (Tilman, 2001; McGill *et al.*, 2006;

78 Violle *et al.*, 2007; Mouillot *et al.*, 2013). These organismal traits are used as currency

79 in the comparisons made among sets of species, often as a measure of functional

diversity (Walker, Kinzig & Langridge, 1999; Tilman, 2001; McGill *et al.*, 2006). Since traits affect ecosystem processes, a functional approach to studying biodiversity is essential to further our understanding of mechanisms and historical–evolutionary processes that have shaped current patterns of biodiversity (Loreau *et al.*, 2001; Hooper *et al.*, 2002; McGill *et al.*, 2006). Most advances in understanding the evolution of functional traits and the mechanisms of species (and trait) assembly have come from studies conducted in terrestrial communities, particularly plant communities (Webb, 2000; Webb *et al.*, 2002; Reich *et al.*, 2003; Ackerly, 2009). The study of plant ecology and evolution has set the basis for the relationship between diversity and ecosystem functioning (Tilman *et al.*, 1997; Tilman, 2001), the measure of functional attributes (Diaz, Cabido & Casanoves, 1998; Westoby & Wright, 2006), the concept of traits (Violle *et al.*, 2007) and the mechanisms of local species pools and trait assembly (Webb, 2000; Webb *et al.*, 2002; Ackerly, 2009). In the sea, only a handful of studies have examined the evolution of functional traits through time (Vermeij, 1977; Jablonski & Sepkoski, 1996), mostly for assemblages inhabiting coral reefs (e.g. Wood, 1999; Goatley, Bellwood & Bellwood, 2010; Bellwood, Goatley & Bellwood, 2016).

For fish species, life-history traits linked to food acquisition and locomotion mediate species ecological roles and influence ecosystems processes (Winemiller, 1991; Holmlund & Hammer, 1999; Mouillot *et al.*, 2013, 2014; Winemiller *et al.*, 2015). Fish traits have also been fundamental to the evolution and diversification of entire fish lineages on coral reefs (Cowman, Bellwood & van Herwerden, 2009; Price *et al.*, 2011). Although coral reefs present an extremely rich fish assemblage with at least 50 evolutionary transitions to reef-dwelling within Acanthomorpha (spiny-rayfinned fishes) alone (Price *et al.*, 2014), some families (e.g. butterflyfishes – Chaetodontidae, wrasses and parrotfishes – Labridae, surgeonfishes – Acanthuridae, angelfishes – Pomacanthidae, damselfishes – Pomacentridae, cardinalfishes – Apogonidae) are considered typical 'reef' fish families with most species being dependent on coral reef environments across the globe (e.g. Bellwood, 1996; Cowman, 2014). Several of these families have formed the core focus of recent studies that characterize how particular species traits map onto a reconstructed phylogenetic hypothesis (e.g. Bellwood *et al.*, 2010; Price *et al.*, 2011; Frédérich *et al.*, 2013; Lobato *et al.*, 2014), and how they correlate with the observable evolutionary history of a group of species. However, it remains unclear whether any of these traits can be linked to the processes promoting speciation, extinction, or the assembly of local species pools. Here we use new and

114 updated life-history trait reconstructions of some of these core reef-associated fish

115 families, as well as re-analyses of published reconstructions, better to understand

116 evolutionary patterns that have led to the functional diversity found on coral reefs today.

117 We further discuss patterns reported in other fish families found on coral reefs that

118 might be influenced by different evolutionary processes but for which we have less

119 information. We provide future directions to this emerging field of functional

120 phylogenetics. Moving forward, a combination of phylogenetic and functional

121 assessment methods will improve our understanding of the mechanisms that shape

122 species assemblages, particularly the extraordinarily rich communities associated with

123 coral reefs.

124

125 **II. THE EVOLUTION OF FEEDING MODES OF REEF FISHES**

126 The evolution of feeding modes has been an important topic in the origins of modern

127 coral reef assemblages (Bellwood *et al.*, 2015). The distinctness of a 'reef-like'

128 assemblage in the fossil record is not only signalled by the taxonomic make-up of a

129 *lagerstätten* (Bellwood, 1996), but also by the functional attributes of fossils (Goatley *et*

130 *al.*, 2010; Bellwood *et al.*, 2014*b*). Particularly interesting are those that indicate the

131 presence of potentially herbivorous taxa (Bellwood *et al.*, 2014*a*), precursor lineages to

132 modern herbivores and detritivores that provide critical functions on modern coral reefs

133 (Hoey & Bellwood, 2008; Bonaldo, Hoey & Bellwood, 2014). Traditionally, the groups

134 that are presently the most conspicuous and abundant in reef habitats have well-resolved

135 (but still incomplete) dated phylogenies and have garnered the most interest in the

136 evolution of feeding modes. Examples include the families Chaetodontidae, Labridae,

137 Pomacanthidae, and Pomacentridae. While these families are considered classic 'coral

138 reef' fish families, they also contain species that are abundant on sub-tropical and

139 temperate rocky reefs as well as other non-reef habitats.

140   The wrasse family Labridae, including the parrotfish and odacid lineages

141 (Westneat & Alfaro, 2005), has been the most popular reef fish family for trophic

142 exploration (Westneat, 1995; Westneat *et al.*, 2005; Alfaro *et al.*, 2009; Cowman *et al.*,

143 2009; Kazancioglu *et al.*, 2009; Price *et al.*, 2011; Lobato *et al.*, 2014). There has been a

144 progressive increase in the phylogenetic resolution of this family and its major lineages

145 over the past decade (Bernardi *et al.*, 2004; Westneat & Alfaro, 2005; Read, Bellwood

146 & Van Herwerden, 2006; Cowman *et al.*, 2009; Cowman & Bellwood, 2011; Choat *et*

147 *al.*, 2012) although sampling remains incomplete (Cowman, 2014). With over 600

148   species (Parenti & Randall, 2011), labrids and parrotfish represent one of the most

149   diverse reef fish taxonomic groups, second only to the Gobiidae in species richness on

150   coral reefs. Within the family Labridae there is an array of feeding modes (Fig. 1), both

151   specialized and generalist, found globally across coral reef ecosystems. These include

152   gastropod feeders, foraminifera feeders, herbivores, piscivores, planktivores,

153   corallivores and obligate fish cleaners (Wainwright *et al.*, 2004; Bellwood *et al.*, 2006).

154   The rise of the more-specialized feeding modes in Labridae – foraminifera, coral

155   mucous, plankton and ectoparasite feeders (fish cleaners) – dates to the

156   Oligocene/Miocene epoch from 30 to ~7.5 million years ago (Ma; Cowman *et al.*,

157   2009). This second wave in trophic origination comes after an initial establishment of

158   generalist feeding modes (gastropod feeding, piscivory and herbivory) in the

159   Paleocene/Eocene, and appears linked to the expansion of scleractinian-dominated

160   reefs. The evolution of trophic novelty and functional morphological diversity within

161   Labridae occurred more rapidly for those species inhabiting coral reefs (assuming more

162   competition and resource diversity), in comparison to non-reef species (Price *et al.*,

163   2011). While reef occupation is also linked to higher diversification within families

164   (Cowman & Bellwood, 2011), species richness and morphological disparity do not

165   seem to be correlated within lineages (Price *et al.*, 2015).

166   Despite the outstanding diversity of trophic groups found in labrids, certain

167   feeding modes are highly conserved within lineages (Fig. 1). For instance, the variety of

168   modes of herbivory/detritivory (browsing, scraping and excavating) are mostly

169   restricted to the parrotfish clade (Scarini), a lineage that emerged during the early

170   Eocene 48.9 Ma (Cowman *et al.*, 2009). Macroalgae browsing is probably the ancestral

171   mode of herbivory within parrotfish (Cowman *et al.*, 2009), which has been retained in

172   the Atlantic restricted *Sparisoma* genus, followed by the origin of 'excavating' in

173   *Bolbometopon* and *Chlorurus* genera (28.8 and 7.4 Ma), and finally 'scraping' in the

174   *Scarus/Hipposcarus* lineage (11.8 Ma). The evolution of excavating and subsequently

175   scraping culminated in the critical processes we see today governing reef dynamics: the

176   recycling of reef sediment and reef calcium carbonates, and the grazing of algae

177   (Bonaldo *et al.*, 2014). Over the last 10 million years (Myr) there has been great

178   diversification within the parrotfish group (see Fig. 1), leading to species-rich clades

179   that appear to be associated with a switch to relatively low-quality food ingestion

180   (Lobato *et al.*, 2014). In the *Scarus* genus alone, there are 53 species (Parenti &

181   Randall, 2011). Herbivory has also arisen in the hypsigenyines clade: *Pseudodax*

182 *moluccanus* (~30 Ma), *Odax pullus*, *O. cyanoallix* (~10 Ma) and *Neodax balteatus* (~5

183 Ma), although most are found on temperate rocky reefs.

184   Foraminifera feeding, coral feeding and fish cleaning are the most recent feeding

185 strategies in the Labridae family and arose within the crown group julidines (Cowman

186 *et al.*, 2009). Foraminifera feeding evolved approximately 15 Ma being highly

187 conserved across the *Macropharyngodon* lineage. Coral feeding evolved within the

188 labrichthyines (~20 Ma; *Larabicus*, *Diproctacanthus*, *Labropsis*, *Labrichthys* genera),

189 as did obligate fish cleaning (less than 10 Ma), both feeding modes being conserved

190 within lineages. Yet fish cleaning – obligate, facultative and by juveniles – has evolved

191 independently 26–30 times within the Labridae family as a whole (Baliga & Law,

192 2016). While cleaning behaviour by juveniles and facultative cleaning appear to be a

193 much more labile trait (Baliga & Law, 2016), members of the *Labroides* lineage are the

194 only species in Labridae that are specialized to obligate fish cleaning as adults. In the

195 *Labroides* lineage, fish cleaning as adults evolved only once and is derived from a

196 coral-feeding lineage in labrichthyines (~9 Ma; Fig. 1). Possibly, the morphological

197 adaptations required to feed on such a specialized diet as ectoparasites were only

198 possible through the already highly adapted coral feeders in the labrichthyines. Within

199 butterflyfishes several species do clean as juveniles (and some even as adults;

200 facultative cleaners), and this habit has also evolved in different clades (*Heniochus*,

201 *Chaetodon* and *Johnrandallia*).

202   The expansion of reef habitat in the Miocene appears to be important in the

203 functional evolution of many other associated lineages. In the family Chaetodontidae

204 (butterflyfishes and bannerfishes), a switch to coral reef habitat appears to have

205 underpinned elevated cladogenesis of the genus *Chaetodon* (90 species), with

206 subsequent multiple origins (five times) of corallivory within the family (Fig. 2;

207 Bellwood *et al.*, 2010). Obligate corallivory evolved rather recently, over the last 10

208 Myr (15.7–3.2 Myr, Bellwood *et al.*, 2010), with most species feeding on hard corals

209 and some on soft coral. This feeding mode first appeared in the *Chaetodon* clade C3,

210 around ~15 Ma (Fig. 2). Within this clade, the majority of taxa are obligate corallivores,

211 exhibiting strong association to the reef substrate (Bellwood *et al.*, 2010). Around 8 Ma

212 this feeding mode evolved in clade 4 (C4 in Fig. 2), although in this lineage species are

213 obligate soft coral feeders and represent significantly fewer lineages. Corallivory can be

214 an extremely specialized diet to the point of species feeding on only a couple of coral

215 species, or ingesting specific parts of the coral, or even feeding only on coral mucous

216 (Berumen & Pratchett, 2008; Cole, Pratchett & Jones, 2008). This move to relatively

217 low-quality food (algae, detritus, sponges and corals) may have accelerated

218 diversification in different reef fish clades (Acanthuroidei, Labridae, Pomacentridae and

219 Chaetodontidae), mediated by ecological opportunity to fill available niche-space

220 (Lobato *et al.*, 2014). Ecological constraints might also lead to diet shifts within

221 lineages, as documented for the *Parachaetodon* lineage. Departure of *Parachaetodon*

222 from a coral-based diet to omnivory could be explained by coral decline in a given

223 marine basin (Bellwood *et al.*, 2010). Overall, corallivory evolved very recently and

224 independently across Chaetodontidae, and these shifts may have promoted some

225 diversification within clades, yet significant rate shifts within *Chaetodon* appeared

226 earlier and are linked with a change to coral reef dwelling (Bellwood *et al.*, 2010,

227 Cowman & Bellwood, 2011). Today, butterflyfishes are among the most iconic

228 inhabitants of reefs, closely associated with, and indicative of ecological conditions in

229 coral-dominated environments, in the case of obligate corallivore species (Kulbicki,

230 Bozec & Green, 2005; Pratchett, Berumen & Kapoor, 2014).

231 Although there is exceptional diversity in corallivorous species found within the

232 chaetodontids, corallivory appeared earlier in the Labridae family, ~29 Ma (Fig. 1).

233 According to Bellwood *et al.* (2010), the shift to corallivory identified in

234 Chaetodontidae coincides with a rise in this feeding mode across other reef fish

235 families. This specialization occured in a context of broader modifications that were

236 taking place in reef environments during the Miocene (from ~23 to 5 Ma), including a

237 number of novel reef-fish interactions – foraminifera feeding, fish cleaning, and an

238 increase in detritivory (Harmelin-Vivien, 2002). This revolution in the reef functional

239 system is concordant with the expansion of *Acropora* and *Pocillopora* corals (Johnson,

240 Jackson & Budd, 2008; Bellwood *et al.*, 2016).

241 Damselfishes (family Pomacentridae) have been present in coral reef ecosystems

242 for at least 50 Myr (Bellwood, 1996; Bellwood *et al.*, 2015), being the third most

243 species-rich family on contemporary reefs, after Gobiidae and Labridae (Cooper, Smith

244 & Westneat, 2009). The pomacentrids comprise over 390 species and might be one of

245 the most successful radiations of coral reef fishes, being diverse, locally abundant

246 (Cooper & Westneat, 2009; Frédérich *et al.*, 2013), and occupying different trophic

247 niches (Cooper *et al.*, 2009, 2017). Dietary behaviour appears to be the main driver of

248 morphological evolution in damselfishes (Frédérich *et al.*, 2008; Cooper & Westneat,

249 2009; Aguilar-Medrano *et al.*, 2011; Frédérich & Vandewalle, 2011). Indeed, similar

trophic strategies (i.e. pelagic, intermediate and benthic feeding) and morphologies (oral

jaw shape and body size) evolved repeatedly across Pomacentridae subclades over the

last 20 Myr. The diversity of trophic strategies and ecomorphological traits within this

family can be attributed to convergent radiations throughout its phylogenetic history,

possibly driven by competition, functional constraints and the regionalization of coral

reefs (Frédérich *et al.*, 2013). This iterative ecological diversification (predictable

patterns in the evolution of phenotypic traits; Losos, 2011) also appears to mediate

constant rates of cladogenesis among clades in Pomacentridae (Frédérich *et al.*, 2013).

Interestingly, convergence in ecomorphological traits has also been observed in the

evolution of triggerfishes (family Balistidae) with distantly related species that are part

of the same guild presenting similar skull and jaw muscle structures (McCord &

Westneat, 2016).

The evolutionary history of marine angelfishes (Pomacanthidae) spans at least 38

Myr (Bellwood, van Herwerden & Konow, 2004; Gaither *et al.*, 2014). Like

chaetodontids, pomacanthids represent a conspicuous element of reef assemblages

across the globe (Allen, Steene & Allen, 1998). The family displays a diverse ecology,

with striking variations in body size, colour patterns, reproductive systems and diets that

range from herbivory to planktivory (Bellwood *et al.*, 2004). Pomacanthids also contain

unique functional novelties (Konow & Bellwood, 2005) that allow the protrusion of the

lower jaw, a rare feature in teleost fishes (Westneat & Wainwright, 1989). Jaw

protrusion was key to the evolution of predator–prey interactions of spiny-rayed fishes

(acanthomorphs) over the last 100 Myr (Bellwood *et al.*, 2015). During this period,

spiny-rayed fishes have become dominant in fish assemblages while the extent of the

premaxilla protrusion increased across lineages, enhancing their ability to catch prey

(Bellwood *et al.*, 2015). In pomacanthids, further jaw modifications have allowed the

closure of the jaw once protruded, creating a 'grab-and-tear' action (Konow &

Bellwood, 2005). This grab-and-tearing feeding mode has appeared only once in the

evolutionary history of the family (Konow & Bellwood, 2011). The combination of

variations in gut morphology and disparities in species body size has resulted in the

evolution of a range of trophic modes within Pomacanthidae (Konow & Bellwood,

2011). The large and robust bodies (with strong bites) of *Pomacanthus* species enabled

the utilization of sponges and tunicates as food items. By contrast, small-bodied

Centropyge [*Xiphypops*] feed on delicate foliaceous algae through a combing or

shearing strategy (Konow & Bellwood, 2011). This genus, along with its sister-taxon

284 *Genicanthus* has experienced rapid diversification and represents 25% of extant

285 angelfish diversity (88 species) (Allen *et al.*, 1998; Konow & Bellwood, 2011). In their

286 Indo-Pacific angelfish study, Konow & Bellwood (2011) found that *Genicanthus*

287 exhibited restricted mouth movements, and its divergent feeding mode within

288 Pomacanthidae corresponds to a functional reversal to planktivory (Howe, 1993; Elliott

289 & Bellwood, 2003). This dietary shift to an ancestral suction-feeding mode (Lauder,

290 1982) will be discussed in Section III.

291

292 **III. WATER COLUMN USE AND SHIFTS TO PLANKTIVORY**

293 The level in the water column occupied by a fish species is critical for determining its

294 ecological niche as it influences the set of potential prey items available to consumers as

295 well as patterns of resource use. Evolutionary shifts in water column use can be found

296 across several different reef fish families (e.g. Epinephelidae, Labridae, Kyphosidae,

297 Lutjanidae, Pomacanthidae and Pomacentridae). These shifts require morphological and

298 behavioural adaptations, which may include a slender fusiform body, and a deeply

299 forked caudal fin for swimming and feeding in mid-water on zooplankton (Randall,

300 1967). These changes usually represent departures from the typical morphology of the

301 family (Randall, 1967). Nevertheless, with recent molecular phylogenies it is now

302 possible to explore shifts in water column use in a comparative framework, combining

303 phylogenies with morphology (e.g. Friedman *et al.*, 2016; Cooper *et al.*, 2017).

304   It turns out that in many cases, planktivorous species described as separate genera

305 due to different morphologies are in fact nested within other genera (Fig. 3). Examples

306 include the mid-water planktivore *Paranthias* within the bottom-related *Cephalopholis*

307 (Craig & Hastings, 2007); *Clepticus* within *Bodianus* (Santini, Sorenson & Alfaro,

308 2016); *Sectator* within *Kyphosus* (Clements & Knudsen, 2016); *Ocyurus* genus placed

309 within *Lutjanus* (Gold, Voelker & Renshaw, 2011) and *Genicanthus* within *Centropyge*

310 in a secondary functional reversal to planktivory (Bellwood *et al.*, 2004; Konow &

311 Bellwood, 2011; Gaither *et al.*, 2014). Even the entirely planktivorous Caesionidae

312 family is now placed within Lutjanidae (Miller & Cribb, 2007). Within Labridae,

313 planktivory appeared in at least three independent lineages – *Cirrhilabrus* (~21 Ma),

314 *Clepticus* (~12.4 Ma), and *Pseudocoris* (~7.2 Ma), all during the Miocene epoch (Fig. 1;

315 Cowman *et al.*, 2009), with each origin correlated with a concomitant increase in jaw

316 transmission coefficients (Westneat *et al.*, 2005). For Pomacentridae, Cooper *et al.*

317 (2017) found that pelagic-feeding damselfishes (planktivores) are strongly differentiated

318   from extensively benthic-feeding species (omnivores and herbivores) by their jaw

319   protrusion ability, upper jaw morphology and the functional integration of upper jaw

320   protrusion with lower jaw abduction. The surgeonfishes (family Acanthuridae) also

321   exhibited strong morphological convergence with zooplanktivorous species evolving

322   slender bodies, reduced facial features, smaller teeth and weakened jaw adductor

323   muscles when compared to their grazing relatives (Friedman *et al.*, 2016). Among

324   haemulids, Price *et al.* (2013) also found that species that feed on zooplankton in the

325   water column present a slender body shape and higher caudal fin aspect ratios.

326   These diet shifts (transitions to planktivory) may represent cases in which

327   ecological opportunity for the exploitation of different resources drives speciation and

328   adaptation (e.g. Bellwood *et al.*, 2004; Lobato *et al.*, 2014). In damselfishes

329   (Pomacentridae), the story appears more complex with multiple transitions having taken

330   place in several ways (Fig. 4). We observe shifts from bottom to higher water column

331   use exemplified by *Amblyglyphidodon* shifting to mid-water within *Neoglyphidodon*, a

332   bottom-dwelling clade. But the reverse is also reconstructed in the *Dascyllus* lineage,

333   with a shift to a bottom-dwelling habit within the larger *Chromis* clade, which are

334   generally higher water-column users (although further phylogenetic sampling of

335   *Chromis* may change this pattern). In general, such shifts have been accompanied by

336   modifications in body shape (see Fig. 3) and a shift to schooling behaviour in the water

337   column. Within the butterflyfishes (Chaetodontidae), transitions have occured from

338   bottom dwelling to the water column exemplified by the *Chaetodon sedentarius–*

339   *miliaris* clade, amidst an otherwise bottom-dwelling *Exornator* subgenus.

340   In Pomacentridae, transitions have occurred multiple independent times across the

341   family's evolutionary history, maintaining constant cladogenesis rates through time

342   (Frédérich *et al.*, 2013) but with some variation among crown lineages (Cowman &

343   Bellwood, 2011; Fig. 4). These transitions are also associated with iterative radiations in

344   subclades, and the ability to exploit different sets of resources: zooplankton in the water

345   column; filamentous algae or coral polyps on the substratum; small benthic

346   invertebrates and algae in varying proportions (Cooper & Westneat, 2009; Frédérich *et*

347   *al.*, 2009, 2013; Cooper *et al.*, 2017). Diversification over the last 10 Myr of the genus

348   *Amphiprion* (clownfishes, see Fig. 4), a bottom-dwelling clade, appears to be

349   significantly higher than background diversification rates for the entire family (Cowman

350   & Bellwood, 2011). This increased diversification rate may have been promoted by the

351   symbioses with sea anemones that characterize this genus (Allen, 1972; Litsios *et al.*,

2012), although geographic replication of radiations might also play a potential role (Litsios *et al.*, 2014). Similar to *Amphiprion*, the coral-dwelling genus *Gobiodon* has diversified in the last 10 Myr in a mutualistic association with *Acropora* corals (Duchene *et al.*, 2013). While these two cases of mutualistic association are a relatively recent phenomenom, the relationships between fishes and the reef substratum have played out over an extended evolutionary history.

The late Cretaceous marks the rise of stem lineages of many modern reef fish families (Near *et al.*, 2013; Bellwood *et al.*, 2015). It is also during this period that morphological changes accompanying the diversification of acanthomorph fishes would have paved the way for the future fish assemblages found on coral reefs. The Paleocene and Eocene epochs (66–34 Ma) represent a phase in the evolutionary history of reef systems where the crown fossil precursors of modern acanthomorph fish families had both the geographic proximity and the morphological proclivity to form the foundation of the modern coral reef fish assemblage (Bellwood *et al.*, 2015). The origins and crown diversification of many functional guilds (e.g. herbivory in surgeonfishes and rabbitfishes, scraping and excavating in wrasses) are most likely associated with the rise of scleractinian-dominated coral reefs (Wallace & Rosen, 2006), allowing rapid expansion into new niche space (Bellwood, 2003; Goatley *et al.*, 2010; Wainwright *et al.*, 2012; Bellwood *et al.*, 2015). But the reverse may also be true. There is evidence to suggest that the movement of fishes into shallow water areas and the expansion of herbivory paved the way for corals to invade what we now see as the highly productive reef flat of a modern coral reef system (Wood, 1999; Bellwood *et al.*, 2016). Modern groups such as scraping parrotfishes and corallivorous butterflyfishes appeared in the Neogene (23–3 Ma), which coincided with diversification in several coral groups (e.g. *Acropora*) from ~20 Ma onwards. The evolutionary history of reef fishes over the last 5 Myr has been mainly decorative – 'baubles on the tree of life', as coined by Bellwood *et al.* (2015) – characterized by new combinations of colours and shapes in fish species. Despite the appearance of new colours and shapes that accounted for some diversification during this time, there appears to be no further functional differentiation in reef fishes or new functional modes occupied (e.g. Labridae; Cowman *et al.*, 2009).

IV. THE EVOLUTION OF BODY SIZE IN REEF FISHES

Body size is one of the most important traits in ecological studies, being related to other parameters such as geographical distribution (Blackburn, Gaston & Loder, 1999; Luiz *et*

386 *al.*, 2013), temperature, metabolism (Brown *et al.*, 2004; Barneche *et al.*, 2014),

387 abundance (White *et al.*, 2007), and even vulnerability to extinction (Reynolds *et al.*,

388 2005; Cheung, Pitcher & Pauly, 2005; Olden, Hogan & Zanden, 2007; Bender *et al.*,

389 2013*a*). Additionally, body size is commonly used as a proxy for many life-history

390 traits, such as longevity, reproductive output, range size (Reynolds, Jennings & Dulvy,

391 2001) and other ecological features, such as type and size of prey that can be consumed

392 and predator-avoidance abilities (Peters, 1986; LaBarbera, 1989; Harmon *et al.*, 2010).

393 Across the ray-finned fish there appears to be an overarching link between the rate of

394 body-size evolution and the rate of lineage diversification (Rabosky *et al.*, 2013).

395 Historically, it seems that smaller-bodied reef fish species were least able to colonize

396 distant habitats after past climatic fluctuations during the Quaternary (Ottimofiore *et al.*,

397 2017), reinforcing this trait as an important determinant of biodiversity patterns in reef

398 environments. While body size in reef fishes has been extensively studied from an

399 ecological perspective (reviewed by Kulbicki, Parravicini & Mouillot, 2015) it has yet

400 to be explored for its evolutionary and phylogenetic significance.

401   Here we mapped body size distributions onto the Labridae family phylogeny (Fig.

402 5). Most labrids are of medium size (10–40 cm; seen in green shades in Fig. 5). Larger

403 sizes were mainly observed in the tribes Hypsigenyini, Cheilini and Scarini, while the

404 smaller body sizes appeared in *Pseudocheilinus* and in some clades within the julidine

405 crown group. The humphead wrasse (*Cheilinus undulatus*) stands out as the largest

406 labrid, reaching up to 230 cm, while *Hemigymnus melapterus* reaches the largest sizes

407 (~60 cm) within the crown julidine clade. There seems to be no relationship between

408 body size and lineage age within labrids, and both large and small body sizes appear

409 multiple times within the clades of mid-sized fishes. Nevertheless, the majority of

410 extreme body sizes – largest (red in Fig. 5) and smallest (dark blue) – emerge in

411 lineages that have arisen in the last 10 Myr across the Labridae phylogeny, even though

412 there are few older, small-sized clades that date back to the mid-Miocene.

413   In Pomacentridae, the evolution of body size throughout the phylogeny is related

414 to the appearance of different trophic strategies, with benthic feeders exhibiting smaller

415 optimal sizes when compared with pelagic and intermediate feeders (Frédérich *et al.*,

416 2013). These trophic strategies and consequently body size within damselfishes have

417 undergone multiple convergent radiations possibly shaped by common ecological

418 selection pressures (Frédérich *et al.*, 2013). Although presenting little structural and

419 functional disparity, angelfishes (Pomacanthidae) evolved a wide range of body sizes,

420 which also appears to be strongly related to the trophic evolution of the family (Konow

421 & Bellwood, 2011). The opposite trend was observed for the Tetraodontidae

422 (pufferfishes) with reef-associated lineages presenting lower body size disparity when

423 compared to freshwater species, even though reef environments might have promoted

424 rapid diversification of two pufferfish genera (*Arothron* and *Canthigaster*; Santini *et al.*,

425 2013*a*). Within Chaetodontidae there is low variation in body size, with 80% of all

426 species being within 10 to 20 cm, which might be related to their dependency and

427 specialization for living in complex three-dimensional coral reef habitats.

428

429 **V. HABITAT USE, RANGE SIZES AND BIOGEOGRAPHY OF REEF FISHES**

430 **(1) Habitat use**

431 Habitat-use patterns have had a key role in the evolution of reef fishes. A number of

432 studies have documented ecological radiations of fish clades following the colonization

433 of reef habitats, where the reef complexity provided unique and novel ecological

434 opportunities (Alfaro, Santini & Brock, 2007; Cowman & Bellwood, 2011; Price *et al.*,

435 2011; Santini *et al.*, 2013*a*). The expansion of a complex mosaic of reef habitats during

436 the Miocene has driven elevated cladogenesis across several reef fish clades in

437 Acanthuridae (Lobato *et al.*, 2014), Labridae, Pomacentridae, Chaetodontidae and

438 Apogonidae (Cowman & Bellwood, 2011), Tetraodontiformes (Alfaro *et al.*, 2007;

439 Santini *et al.*, 2013*a*), and Carcharhinidae (Sorenson, Santini & Alfaro, 2014).

440 Bellwood *et al.* (2016) proposed that an increase in the range of habitats occupied, such

441 as reef flats, was related to novel morphologies for increasing swimming ability to cope

442 with hydrodynamic challenges (e.g. high-aspect-ratio pectoral fins in labrids, shift in

443 eye position and caudal peduncle depth in surgeonfishes). The expansion of

444 scleractinian-dominated reef habitats throughout the Miocene can also be associated

445 with the rise of one the most specialized swimming modes within the balistoid fishes

446 (triggerfishes and filefishes) using coupled oscillation or ondulation of paired median

447 fins (Dornburg *et al.*, 2011; Santini, Sorenson & Alfaro, 2013*b*). Reef association also

448 seems to offer some resistance to extinction where lineages with higher reef occupation

449 remain significantly more diverse than expected when faced with high (simulated) rates

450 of extinction (Cowman & Bellwood, 2011).

451   In Haemulidae, habitat use has also influenced the diversification of lineages and

452 extant patterns of diversity. While hard bottom environments are inhabited by few but

453 very speciose haemulid lineages (e.g. *Plectorhinchus*, *Haemulon*, *Anisotremus*), in soft

bottoms there are a greater number of genera, yet with fewer species (Tavera *et al.*, 2012). Haemulids exhibit similar patterns of species richness and ecological diversity both on and off reef habitats. However, those haemulid lineages that are reef associated display increased rates of ecomorphological evolution compared with their counterparts, especially in trophic traits related to prey capture and processing (see Price *et al.*, 2013). A similar pattern is also seen in labrids where tropical reef-associated lineages exhibit faster rates of evolution in trophic ecomorphological space compared to tropical non-reef lineages (Price *et al.*, 2011).

Although there seems to be a congruent pattern of higher ecomorphological diversification associated with groups that present specialized diets such as planktivory, herbivory or invertivory, piscivorous groups may follow different evolutionary paths. By analysing carangoid fishes (jacks, remoras and allies), which include some piscivorous reef-associated species, Frédérich *et al.* (2016) found that a higher rate of morphological diversification is associated with habitat shifts to non-reef environments. These results do not exclude the important role of reef habitats in the early diversification of carangoids during the Eocene, however, it highlights that the major radiation of the group occurred recently in non-reef environments (Frédérich *et al.*, 2016). Similarly, the diversification of grouper lineages (family Epinephelidae) does not seem to be correlated with the expansion of coral habitats in the Miocene and might have been more influenced by global environmental changes during this period (Ma *et al.*, 2016). In contrast to these results, Sorenson *et al.* (2014) found that reef association is significantly correlated with requiem shark diversification, showing that the drivers of diversification for piscivorous reef species are idiosyncratic and deserve greater attention. Multiple transitions between reef and non-reef habitats have also been reported for the piscivorous barracudas (family Sphyraenidae) (Santini, Carnevale & Sorenson, 2015), however, it remains unclear whether these shifts represent significant departures from the background rate of diversification for the group.

Understanding how shifts in habitat use have influenced the rates of morphological and lineage diversification are critical for understanding the functional history of reef systems. In the case of reef occupation, this requires accurate knowledge of the intial transition into shallow-water reef habitat. Using labrids as an example, there is a possible basal shift to reef habitat in the labrid tree when comparing the relatively non-reef-associated hypsigenyine lineage to non-hypsigenyines, which are more reef associated (Cowman *et al.*, 2009). However, given the lack of knowledge of the true

488 sister group to the Labridae (Cowman, 2014), the exact timing of ancestral reef

489 occupation of labrid lineages cannot be known for certain. Yet, there are several labrid

490 fossils in Eocene deposits (50 Ma) that suggest at least proximity to shallow water reef

491 systems (Bellwood, 1996).

492   A broader taxonomic and temporal view of the occupation of ancestral shallow-

493 water reef systems across all Acanthomorpha (spiny-rayed fishes) outlines the deep

494 evolutionary history of reef association and how multiple families have independently

495 transitioned into reef habitat (Price *et al.*, 2014). The study of Price *et al.* (2014)

496 highlights that the colonization of ancestral reef systems by acanthomorph lineages

497 potentially occurred in two waves of invasion either side of the Cretaceous–Paleogene

498 (K–Pg) boundary (~66 Ma). The first wave of invasion possibly took place in the Late

499 Cretaceous (90–72 Ma), and the second occurred during the early Paleogene, following

500 the K–Pg mass extinction (65–56 Ma). These waves of reef invasion might have been

501 related to changes in reef structure and climate (Price *et al.*, 2014). While colonizing

502 new habitats such as the reef environment, fish lineages underwent morphological

503 convergence. Such a process fits the macroevolutionary niche-filling scenario of

504 Ricklefs (2010), where the ecological opportunities found in new habitats promote

505 functional convergence of species and clades, followed by saturation of the

506 morphospace. As the functional space in reef-associated lineages became increasingly

507 saturated, there was a slowdown in the pace of reef invasions by acanthomorphs.

508

509 **(2) Range size and biogeography**

510 Geographical range can be viewed as a property that results from the combination of

511 different species traits (e.g. body size, reproductive mode, trophic group, dispersal

512 potential) subjected to environmental constraints through time. In addition, range size,

513 or space occupancy, is generally associated with commonness or rarity and thus may be

514 related to the vulnerability of species (Connolly *et al.*, 2014; Parravicini *et al.*, 2014; but

515 see Hughes *et al.*, 2014). Despite its relevance, only a handful of studies have explored

516 range size in the context of within-genus evolutionary relationships (Hodge *et al.*, 2012)

517 or species age (Mora *et al.*, 2012). Here we performed a reconstruction of range size,

518 given by the number of grid cells occupied by each species (each $5° \times 5°$ grid cell

519 corresponds to approximately 550×550 km at the equator) across the marine tropics,

520 on a time-calibrated phylogenetic tree for Labridae (Fig. 6). This reconstruction shows

521 that for labrids, range size appears constrained by the geography and size of ocean

522 basins (reviewed by Ruttenberg & Lester, 2015). For example, fishes from Atlantic or

523 Tropical East Pacific (TEP) clades (e.g. members of the genus *Scarus* such as *S.*

524 *guacamaia* and the '*Iridio*' clade among *Halichoeres* such as *H. socialis*; see Fig. 6)

525 tend to have much smaller geographical ranges compared to congeners occurring in the

526 Indo-Pacific. There also appears to be a temperate *versus* tropical range effect. Clades

527 restricted to temperate areas such as the genera *Labrus, Symphodus, Notolabrus,*

528 *Pseudolabrus*, and *Odax* also tend to have small ranges when compared to more tropical

529 clades. Similarly, chaetodontid species with Atlantic and TEP distributions as well as

530 the warm temperate genus *Amphichaetodon* have smaller ranges. These patterns may be

531 related to overall differences in the size of ocean basins, and historical availability and

532 stability of habitats (Ottimofiore *et al.*, 2017), as well as different extinction rates

533 among basins (e.g. O'Dea *et al.*, 2007) and latitudes (Siqueira *et al*., 2016). Estimates of

534 phylogenetic dissimilarity of reef fish assemblages also highlight variations in reef

535 connectivity and provinciality through time (Cowman *et al.,* 2017).

536   Reef fishes vary dramatically in the extent of their geographic distributions

537 (Ruttenberg & Lester, 2015), however, few within-clade analyses of range size are

538 available to date (but see Hodge *et al.*, 2012; Hodge & Bellwood, 2016). The

539 reconstruction of range size in labrids (Fig. 6) highlights many cases of disparate range

540 sizes among sister-species pairs, complexes and clades such as *Thalassoma purpureum–*

541 *virens*, *Coris aygula–flavovittata*, the *Scarus* '*rubroviolaceus*' clade (Fig. 7),

542 *Macropharyngodon meleagris–geoffroy* (Read *et al.*, 2006), and *Anampses* (Hodge *et*

543 *al.*, 2012). Three models of diversification could explain these intriguing cases: the

544 vicariance-based 'successive division' model, the dispersal-based 'successive

545 colonization' model and the 'peripheral budding' model (*sensu* Hodge *et al.* 2012).

546   Although species range sizes are restricted by the size of ocean basins in which

547 they occur, it is possible to expect that older lineages have had more time to disperse,

548 reaching greater geographic range sizes compared to recently diverged species (but see

549 Mora *et al.*, 2012). In addition, a species' body size has been shown to be related to its

550 range size, with large-bodied species exhibiting greater ranges compared to smaller ones

551 (Gaston & Blackburn, 1996; Luiz *et al.*, 2013). The relationship between the age of 303

552 Labridae species and their range size, measured as the number of grid cells occupied by

553 each species, revealed no significant pattern of species range size distributions with

554 lineage age (Fig. 8A, B). This is not surprising given the effects that peripheral

555 speciation and range persistence can have on age–area relationships (Hodge &

16

556   Bellwood, 2015). When a sister-pair approach is taken, in an effort to mitigate

557   peripheral speciation processes (Hodge & Bellwood, 2016), a significant, albeit weak

558   trend emerges between labrid range size and lineage age (Fig. 8C, D; r^2=0.03; N=191;

559   d.f.=1,189; F=5.94; P=0.015), where the minimum range size of sister-species pairs

560   increases linearly with lineage age. When 'basin' (Indo-Pacific + TEP vs. Atlantic) was

561   included as an effect in the regression model, there was also a significant relationship

562   between minimum range size and age, but much more of the variation is explained by

563   the model (r^2=0.18; N=191; d.f.=2,188; F=21.3; P<0.001). This significant result

564   remains when the data are log–log transformed to account for positive skeweness

565   (r^2=0.18; N=191; d.f.=2,188; F=20.9; P<0.001). This basin effect likely reflects the

566   difference in range-size dynamics and biogeographic history of the two regions. Range

567   sizes are far more evenly distributed across a broader size range in the Indo-Pacific

568   compared to the Atlantic (Fig. 8). There was no clear impact of maximum body size

569   (circle size in Fig. 8), or diet on the relationship between minimum range size and age.

570   At least for labrids, species with different body sizes and trophic modes occupy a large

571   spectrum of range sizes across both basins, regardless of age. A similar pattern for

572   trophic mode and range size was found by Luiz *et al.* (2013). A more in-depth temporal

573   view of functional evolution across multiple traits of reef fish assemblages is needed to

574   understand how trait variation is partitioned across geographic and geological scales.

575

576   **VI. FUNCTIONAL EVOLUTION OF REEF FISH ASSEMBLAGES**

577   **(1) Multi-trait comparisons, lineage accumulation and disparity through time**

578   Multi-trait comparisons, from a phylogenetic perspective, presents an opportunity to

579   examine how complex ecological patterns have played out over evolutionary timescales.

580   Examining the relationship between cladogenesis (diversification) and the evolution of

581   phenotypic variation (disparity) can tell us a great deal about how a clade has radiated

582   and the role life-history traits have played in its diversification. In Fig. 9, we synthesize

583   some emerging patterns for the families Labridae, Pomacentridae and Chaetodontidae

584   over the last 60 Myr, based on phylogenetic and trait reconstruction, and estimates of

585   disparity through time.

586   Lineage through time (LTT) plots display the tempo of diversification through

587   time (Fig. 9A). Cowman & Bellwood (2011) proposed that an antisigmodal pattern in

588   Labridae (and potentially in Pomacentridae) may point to a cryptic extinction event (*cf.*

589   Crisp & Cook, 2009) linked to the collapse of ancestral biodiversity hotspots (Renema

590 *et al.*, 2008). Comparatively, the evolution of butterflyfishes has played out over a
591 shorter timescale. With a crown divergence of ~33 Ma the chaetodontids perhaps show
592 less sign of the collapse of ancestral habitat to the west and are tied to the expansion of
593 shallow-water reef systems in the central Indo-Pacific. They display a birth/death
594 pattern of lineage accumulation with a possible rate shift at the base of the crown
595 *Chaetodon* lineage (Cowman & Bellwood, 2011). Nevertheless, the functional
596 evolution of this group reflects a pattern similar to that of labrids where more trophic
597 innovation within lineages occurs in the Miocene.
598   The stacked density plot of ancestral trait reconstructions reflecting trophic
599 evolution and water column use (Fig. 9B) shows the proportion of nodes that were
600 reconstructed with the highest likelihood for each trait examined. In the Labridae, the
601 expansion of herbivory/detritivory and specialized feeding modes begins in the
602 Oligocene and continues into the Miocene, a time that sees massive expansion of coral
603 reefs in the Indo-Pacific. A jump in the number of nodes reconstructed with herbivory
604 and detritivory coincides with the origins of the *Scarus* and *Chlorurus* lineages, which
605 also represents a shift in the rate of lineage diversification (Cowman & Bellwood, 2011)
606 and significant morphological divergence (Price *et al.*, 2011). However, there is only
607 weak support for a relationship between the two (Alfaro *et al.*, 2010). These results
608 mirror those of Cowman *et al.* (2009) which show expansion of novel feeding modes
609 during the Oligocene and Miocene and point to a closer association between wrasses
610 and the reef substratum during this time. Similarly, the origins of corallivory in the
611 butterflyfishes show a signal of expansion in the mid-Miocene coinciding with the
612 evolution of that feeding mode in several independent lineages (Bellwood *et al.*, 2010).
613 Water column use in the Pomacentridae appears to show no consistent pattern in
614 magnitude of transistions through time from bottom dwelling to higher water column
615 users. From the phylogenetic reconstruction (Fig. 4), it is clear that shifts to higher
616 water column use occurred in subclades throughout the phylogeny with only one
617 instance involving a transition back to bottom dwelling in the *Dascyllus* lineage.
618   A positive disparity index through time (DTT) for body size for all three families
619 indicates that the subclade disparity in body size is higher then expected under a
620 Brownian motion model (Fig. 9C). This, along with no evidence of a slowdown in rates
621 of cladogenesis in these groups (Cowman & Bellwood, 2011), shows that in these reef
622 fish families there is little evidence of a single process of adaptive radiation. These
623 disparity methods have been used previously to explore adaptive radiations in cetaceans

(Slater *et al*., 2010), the rodent genus *Rattus* (Rowe *et al*., 2011), and lizards (Harmon *et al*., 2003). Patterns here suggest that body size variation in reef fishes is partitioned within clades more than among clades (although not significantly so). Such a pattern was also found by Frédérich *et al.* (2013) for Pomacentridae body size and jaw morphology. They concluded that such disparity patterns highlight iterative ecological diversification rather than single adaptive radiation. Similarly here, body size patterns in Labridae and Chaetodontidae show far higher disparity within clades than among them, with the pattern most apparent in the Chaetodontidae. Butterflyfishes, however, display little body size variation, so any small changes in body towards the tips will result in higher estimates of disparity. It is interesting to note that Dornburg *et al.* (2011) found a low body shape disparity through time for triggerfishes (family Balistidae), suggesting a pulse of phenotypic and functional innovation early in the history of the group with a subsequent slowdown in shape disparity. They also found that this early morphological disparity was decoupled from lineage diversification in triggerfishes (Dornburg *et al.*, 2011), which reinforces a common pattern in reef fish evolutionary history (Price *et al.*, 2015).

Although non-morphological traits are not commonly examined in this manner, assessments of disparity through time have been useful for examining extinction threat and range size in angiosperms (Davies *et al*., 2011). For the reef fish families examined, as with body size, range size disparity through time shows more disparity within clades than among them and more so toward the tips of the trees (Fig. 9D). This pattern highlights two things: first, more closely related species show larger asymmetries in range size towards the tips. An implication of this pattern could be an observed higher asymmetry in extinction risk as was previously observed in angiosperms (Davies *et al*., 2011). Second, this points towards the influence of peripatric and peripheral isolation mechanisms in speciation of these groups. This supports the relationship between lineage age and geographic range size discussed above (Fig. 8), where a significant relationship is only found in minimum geographic range size of sister pairs (*cf.* Hodge & Bellwood, 2016). Higher asymmetries outside the 95% range in all three families is seen from 20 Ma onward, a pattern concordant with body size disparity, and trophic expansion within the Labridae and Chaetodontidae. Although there are several clades in all three families that have deep-time separation among ocean basins, there is consistently higher disparity in range size within clades than among them.

(2) A phylogenetic and functional approach to community assessment

Functional trait approaches may enlighten the understanding of community assembly patterns and processes (McGill *et al.*, 2006). At the local scale, the analysis of patterns of traits among co-occurring species offers insights into the influence of the link between short-term local processes and those that occur at global and evolutionary timescales (Fig. 10). Moreover, trait-based studies provide the basis to assessments of functional diversity, redundancy or insurance, as well as the provision of services (Mouillot *et al.*, 2013, 2014). Nevertheless, such approaches are conducted at local spatial and time scales, often without an evolutionary perspective. Thus, they can offer only a snapshot of communities, without insight into the totality of mechanisms that have shaped extant reef fish communities. When trait-based approaches are coupled with phylogenetic analyses of local communities, it is possible to assess which species traits have strongly influenced the evolutionary history of regional assemblages and local communities, as well as to uncover the mechanisms of species assembly (Fig. 10; Cavender-Bares *et al.*, 2009; Gerhold *et al.*, 2015).

The main focus of most studies of reef fish communities has been the evolution of traits across lineages (Cowman *et al*., 2009; Bellwood *et al*., 2010; Price *et al*., 2013; Lobato *et al*., 2014), where the evolutionary patterns of specific traits are mapped into a reconstructed phylogeny (in Fig. 10 shown by the phylogeny on the left representing the regional pool of species and its traits). On the other hand, trait-based approaches to the study of local communities combined with phylogenies have been developed under the research area of phylogenetic community ecology (see Webb *et al*., 2002; Cavender-Bares *et al.*, 2009). Such approaches can reveal the processes that have shaped different communities through time (in Fig. 10 shown by the phylogenies on the right depicting the phylogenetic structure of local communities). The transition from regional to local scales occurs across spatial and temporal scales, through the effect of biotic (e.g. species interactions, dispersal limitation, habitat specificity, local population structures) and abiotic filters (e.g. distance from a source pool, temperature, area, habitat availability, etc.). These filters determine the structure of local communities, both phylogenetically and functionally. At the local scale, communities may exhibit the following structures (shown in Fig. 10): phylogenetic and functional clustering (C1); phylogenetic clustering and functional overdispersion (C2); phylogenetic and functional overdispersion (C3); and phylogenetic overdispersion and functional clustering (C4).

691   Investigating the phylogenetic and functional structure of communities enables

692 the identification of the ecological factors that have played a role in structuring

693 communities through evolutionary time. For instance, in Fig. 10, community C1 has

694 been shaped by environmental or biotic filters acting on phylogenetically conserved

695 traits – under the hypothesis of niche conservatism where species with shared ancestry

696 present similar phenotypes (Webb, 2000; Wiens & Graham, 2005; Losos, 2008). Such

697 fish species composition and trait assembly (in C1) could have been structured by the

698 effect of isolation, for instance, filtering related species with a particular trait that

699 facilitates dispersal, colonization and persistence (e.g. body size, rafting capacity; Luiz

700 *et al.*, 2013). Moreover, this structure could result from the selective forces of generalist

701 predators acting on conserved defence traits (Cavender-Bares *et al.*, 2009).

702 Hypothetically, predators could filter closely related species that share a particular

703 swimming or escape ability to persist in local communities.

704   Environmental and biotic filters can also cause phylogenetic overdispersion if

705 selected traits are labile and related species occupy different niches, where ecological

706 divergence is driven by competition (Schluter, 2000; C3 and C4 in Fig. 10). If traits

707 were convergent across lineages, then habitat or biotic filtering would result in

708 functional clustering of communities (seen in C4). For instance, the increased richness

709 patterns of small-bodied fishes in the centre of marine biodiversity may possibly reflect

710 the degree of feeding and microhabitat specialization of species belonging to different

711 lineages (e.g. *Gobiodon*, *Halichoeres*). Furthermore, the effects of past environmental

712 change (over species pools) have certainly shaped contemporary patterns of the

713 phylogenetic and functional structure of communities. In coral reefs, Quaternary climate

714 fluctuations have influenced the geological complexity and availability of coral reef

715 habitats for associated fish fauna with areas of stable refugia being a strong predictor of

716 current richness patterns of reef fishes at a global scale (Pellissier *et al.*, 2014). Such

717 historical processes have shaped the global patterns of phylogenetic and functional

718 structure in reef fish lineages (Ottimofiore *et al.*, 2017). The families Pomacentridae,

719 Chaetodontidae and Labridae exhibited high phylogenetic clustering in the Indo-

720 Australian Archipelago, partly due to vicariance events resulting from reef

721 fragmentation (Leprieur *et al.*, 2016). These tracked responses of assemblages to past

722 environmental and biotic effects may help us understand the capacity of current

723 communities to respond to global changes such as fishing pressure, climate change,

724 habitat loss and species extinctions.

VII. FUTURE DIRECTIONS

The study of coral reef fish traits has included both ecological and phylogenetic approaches. Ecological assessments have covered the functional structure of reef fish communities along gradients of diversity, coral reef area, isolation, sea surface temperature, etc., from local (Guillemot *et al.*, 2011; Micheli *et al.*, 2014) to regional (Halpern & Floeter, 2008; Bender *et al.*, 2013*b*) and up to global scales (Stuart-Smith *et al.*, 2013; Mouillot *et al.*, 2014; Parravicini *et al.*, 2014). These studies have addressed aspects of functional diversity that are important to reef conservation, encompassing functional insurance, redundancy, and ecosystem services (Micheli *et al.*, 2014; Mouillot *et al.*, 2014; Parravicini *et al.*, 2014). In parallel, phylogenetic studies have examined the evolutionary patterns of a variety of traits in reef fish lineages, aligning their findings to key historical and biogeographical events and evolutionary processes that have shaped reef fish functional diversity (Alfaro *et al.*, 2009; Erisman, Craig & Hastings, 2009; Bellwood *et al.*, 2010; Price *et al.*, 2011; Frédérich *et al.*, 2013; Lobato *et al.*, 2014). Community phylogenetics combines ecology with phylogeny to offer a framework to examine the functional history of an assemblage, but also to address how assemblage structure and function are shaped by evolutionary processes.

Only a handful of studies have implemented a community phylogenetic approach to assess coral reef fish communities (e.g. Hubert *et al.*, 2011; Leprieur *et al.*, 2016), and the functional aspect is yet to be integrated. Functional entities, or groups of species with distinct functional trait combinations, have been described in reef fish communities and related to ecosystem processes, functional redundancy, and vulnerability to extinction (Mouillot *et al.*, 2014). The lack of a phylogenetic component in these studies means that while we can identify which species and which functional roles are redundant or vulnerable, we do not know the origin of these functional entities or the evolutionary histories of the trait combination they represent. Future multi-trait phylogenetic assessments will highlight how trait combinations are shared among closely related species and how they are functionally and phylogenetically structured in local and regional assemblage pools allowing for more integrated conservation solutions. Such an endeavour is becoming more achievable with the rapid improvement of molecular data generation for reef fishes and improvements in phylogenetic sampling and resolution. This resolution, combined with knowledge on species traits and distributional patterns across the globe, will make these studies feasible at global scales.

759   In sum, combining phylogenetic and trait-based approaches to the better understanding

760   of ecosystem functioning is an emerging topic and key to the promise of so-called

761   Functional Biogeography (Violle *et al.*, 2014).

762   The presence of specific traits, or trait combinations can influence a species'

763   capacity to respond and adapt to climatic stress, ultimately influencing patterns of

764   dispersal, colonization, speciation and extinction (Puebla *et al.*, 2007; Luiz *et al.*, 2013;

765   Bender *et al.*, 2013*a*; Ottimofiore *et al.*, 2017). Links between several functional traits

766   and accelerated cladogenesis in the most phylogenetically well-sampled reef fish

767   families have been described here, although further sampling of clades with reef and

768   non-reef components still need to be examined to assess the generality of these trends. It

769   is unclear how or if functional 'success' at the macroevolutionary level (high species

770   diversity within functional roles) scales down to the individual level (species

771   abundance). The next frontier in community phylogenetics requires the inclusion of

772   patterns of abundance of co-occurring taxa to examine population-level effects of

773   species-level interactions. While species traits influence the distribution of organisms

774   and the structure of communities, interactions among co-occurring species will

775   influence the presence of traits within communities and evolutionary processes driving

776   speciation and adaptation (Bascompte & Jordano, 2007; Jablonski, 2008; Cavender-

777   Bares *et al.*, 2009). These future studies will help identify the role of abundance at

778   ecological and evolutionary timescales.

779

780   **VIII. CONCLUSIONS**

781   (1) Species functional traits form a link between evolutionary history and the ecological

782   proceses shaping lineages. By mapping functional traits onto species-level phylogenies,

783   we can examine their evolutionary origins and their influence on lineage diversification.

784   This functional view to evolutionary history is important in the study of present-day

785   biodiversity patterns. In the case of modern reef systems, fish functional traits related to

786   food aquistion and locomotion have been important for driving speciation but also in

787   shaping ecosystem processes.

788   (2) Ancestral trait reconstruction for feeding modes in labrids showed an early

789   establishment of herbivory and subsequent origins of detrivory in parrotfishes, a critical

790   reef process. Trophic evolution can be conserved within clades as in labrids, or reflect

791   multiple independent orgins such as corallivory in butterflyfishes. From reconstructions

792   across several groups we show examples of independent transitions to planktivory that

793   may represent cases in which ecological opportunity for the exploitation of different

794   resources drives speciation and adaptation.

795   (3) Body size is often used as a proxy for other life-history characteristics, but its

796   evolutionary history is not well studied at the species level. The evolution of body size

797   in the family Labridae shows no relationship with lineage age, with both large and small

798   body sizes appearing multiple times within clades of mid-sized fishes. Extremely large

799   and small body sizes arise in disparate lineages mostly in the last 10 Myr. Labridae and

800   Chaetodontidae show higher body size disparity within clades than among them through

801   time. In the Pomacentridae, body size evolution appears closely linked with the

802   convergent evolution of different trophic strategies among clades.

803   (4) The reconstruction of range size in Labridae revealed that ranges are mostly

804   constrained by the geography and size of ocean basins. When accounting for peripheral

805   speciation processes in sister pairs, we found a significant relationship between labrid

806   range size and lineage age. The reconstruction of disparate ranges among sister-species

807   pairs and species complexes and range size disparity through time highlights potential

808   vicariant processes through isolation in peripheral locations with subsequent range

809   expansion.

810   (5) Ecological approaches to the study of life-history traits in reef-associated fishes have

811   unveiled the functional structure of communities across biodiversity and environmental

812   gradients. Evolutionary approaches mapping the phylogenetic origins of species groups

813   within reef communities correlate to historical processes acting on the distribution of

814   reef habitat through time. With the increasing availability of phylogenies (with

815   complete or nearly complete taxon sampling) a combined phylogenetic and functional

816   approach will allow a number of evolutionary and ecological questions to be addressed

817   in the near future that will certainly help us to uncover the mechanisms of community

818   assembly over space and time.

819

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829 Excellence for Coral Reef Studies.
830

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Figure Legends

Fig. 1. Diet and feeding mode reconstruction mapped on a time-calibrated phylogenetic tree for 303 (of ~630) species of wrasses and parrotfishes (family Labridae) (Cowman & Bellwood, 2011 combined with Choat *et al.*, 2012). Colour-coding depicts different feeding modes of adults. The timescale is dated in million years (Myr) before present. Pie graphs within symbols represent the probability of the ancestral state in each node. Clade abbreviations: Hyp, Hypsigenyines; Lb, Labrines; Chl, Cheilines; Scr, Scarines; Cirr, *Cirrhilabrus*; Lbr, Labrichthyines; Mcr, *Macropharyngodon*. Reconstruction was conducted using maximum likelihood in Ape package (Paradis *et al.*, 2004), R software. Fish images: J.P. Krajewski, J.E. Randall, and L.A. Rocha.

Fig. 2. Reconstruction of coral feeding in a time-calibrated phylogenetic tree for 95 (of 127) species of butterflyfishes and bannerfishes (family Chaetodontidae) (Cowman & Bellwood, 2011). Colour-coding is related to species diets. The timescale is dated in million years (Myr) before present. Pie graphs within symbols represent the probability of the ancestral state in each node. Clade abbreviations: Bn, bannerfishes; Pr, *Prognathodes*; C1, 2, 3 & 4, *Chaetodon*. Reconstruction was conducted using maximum likelihood in Ape package (Paradis *et al.*, 2004), R software. Images from Kuiter (2002).

Fig. 3. Three examples of independent transitions to planktivory in reef fish lineages. Note that specializations for feeding in mid-water on zooplankton, such as a slender fusiform body, and a deeply forked caudal fin represent departures from the typical morphology of the genus. Trees used: *Bodianus* clade (Santini *et al.*, 2016), *Kyphosus* (Clements & Knudsen, 2016) and *Cephalopholis* clade (Ma *et al.*, 2016).

Fig. 4. Reconstruction of water column use on a time-calibrated phylogenetic tree for 206 (of 373) damselfish species (family Pomacentridae) (Frédérich *et al.*, 2013). Pie graphs within symbols represent the probability of the ancestral state (position in the water column) at each node, with colour-coding representing fish species that live close to the bottom (blue), and fish that generally form aggregations well above the bottom to feed on zooplankton (red). The timescale is dated in million years (Myr) before present.

1342 Reconstruction was conducted using maximum likelihood in Ape package (Paradis *et*

1343 *al.*, 2004), R software. Fish pictures: J.P. Krajewski and L. Tyk.

1344

1345 **Fig. 5.** Reconstruction of body size on a time-calibrated phylogenetic tree for 303

1346 species of wrasses and parrotfishes (family Labridae) (Cowman & Bellwood, 2011

1347 combined with Choat *et al.*, 2012). The colour gradient represents variation in species

1348 body size, from small to large body sizes (blue to red shades). Body size values were

1349 log-transformed prior to reconstruction. Pictures are representative of those fish species

1350 larger than 80 cm or smaller than 8 cm in length. The timescale is dated in million years

1351 (Myr) before present. Reconstruction was conducted using maximum likelihood in Ape

1352 package (Paradis *et al.*, 2004), R software. Fish pictures: J.P. Krajewski, J.E. Randall,

1353 and L.A. Rocha.

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1355 **Fig. 6.** Reconstruction of range size (given by the number of grid cells of 550×550 km)

1356 in a time-calibrated phylogenetic tree for the Labridae (Cowman & Bellwood, 2011

1357 combined with Choat *et al.*, 2012). Colour-coding represents a gradient from 1 to 258

1358 occupied grid cells. The timescale is dated in million years (Myr) before present.

1359 Reconstruction was conducted using maximum likelihood in Ape package (Paradis *et*

1360 *al.*, 2004), R software. Pictures of representative fish with large and small range sizes

1361 are shown. Fish pictures: J.P. Krajewski, J.E. Randall, and L.A. Rocha.

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1363 **Fig. 7.** Maps of geographical ranges of sister species that present disparate sizes. Range

1364 data comes from IUCN database. Maps are shown in Mollweide projection.

1365

1366 **Fig. 8.** The relationship between age and range size across 303 Labridae species,

1367 divided into (A) Indo-Pacific plus Tropical Eastern Pacific (TEP) and (B) Atlantic

1368 Ocean basins. There was no significant relationship between all species ages and their

1369 geographic range. (C, D) **T**he relationship between minimum geographic range and

1370 lineage age of species sister pairs for the same two regions, in an approach to account

1371 for peripheral isolation processes (Hodge & Bellwood, 2016). A significant relationship

1372 was found between log minimum range size and log lineage age of sister pairs, with a

1373 significant effect linked to ocean basin differences (r^2=0.18; N=191; d.f.=2,188;

1374 F=20.9; P<0.001). Circles are proportional to species maximum body size and colour-

1375 coding represents feeding modes.

1376

1377 **Fig. 9.** Multi-trait patterns through time for the families Labridae, Pomacentridae and

1378 Chaetodontidae. (A) Lineage through time (LTT) plot displaying the log number of

1379 lineages arising through time. LTT plots were constructed from the time-calibrated

1380 phylogenies displayed in Figs 1, 2 and 4 (see text for details). Eo, Eocene; Oli,

1381 Oligocene; Mio, Miocene; PP, . (B) Stacked density plot of ancestral trait

1382 reconstructions reflecting trophic evolution in the family Labridae; water column use in

1383 the family Pomacentridae; and corallivory in the family Chaetodontidae. For the

1384 Labridae, feeding modes are reclassified as generalist modes (Gen: general carnivory,

1385 piscivory, omnivory), herbivory and detritivory (H/D: browsing, scraping, excavating)

1386 and specialized feeding modes (Spec: coral mucous feeding, obligate cleaning,

1387 foraminifera feeding and planktivory). In the Chaetodontidae node density plot, nodes

1388 that are reconstructed as corallivores contain both hard- and soft-coral-feeding lineages.

1389 (C) Mean subclade disparity through time (DTT) for body size data (solid line) for each

1390 of the focal families. The dashed line indicates the median subclade DTT based on

1391 1,000 simulations of character evolution on each reef fish family phylogeny under

1392 Brownian motion. The shaded area indicates the 95% DTT range for the simulated data.

1393 Body sizes were log-transformed prior to analyses. (D) Mean subclade disparity through

1394 time (DTT) for range size (solid line) for each family. Ranges size is calculated as the

1395 number of 550×550 km grid cells occupied by each species. As for body size disparity

1396 seen in C, the dashed line indicates the median and the shaded area the 95% DTT range

1397 based on 1,000 simulations under Brownian motion. DTT analyses were conducted in R

1398 using functions from the Geiger package (Harmon *et al.*, 2008). For both body size and

1399 range size disparity, we calculated the disparity index (DI), which quantifies the relative

1400 disparity of a clade compared with the expectation under the null Brownian motion

1401 model (see Harmon *et al.*, 2003). Positive DI values indicate higher disparity than

1402 expected under the null model.

1403

1404 **Fig. 10.** A framework for trait-based approaches to studies of ecological communities

1405 coupled with phylogenies (or phylogenetic data) and abundance data. The phylogeny on

1406 the left corresponds to a hypothetical regional pool of species and the phylogenies on

1407 the right represent the local structure of communities (C1, C2, C3 and C4). Each

1408 structure reveals the effect of different mechanisms over spatial and temporal scales on

1409 the regional pool of species (see text for further information). Different coloured and/or

1410 shaped fish depict the presence of different traits.

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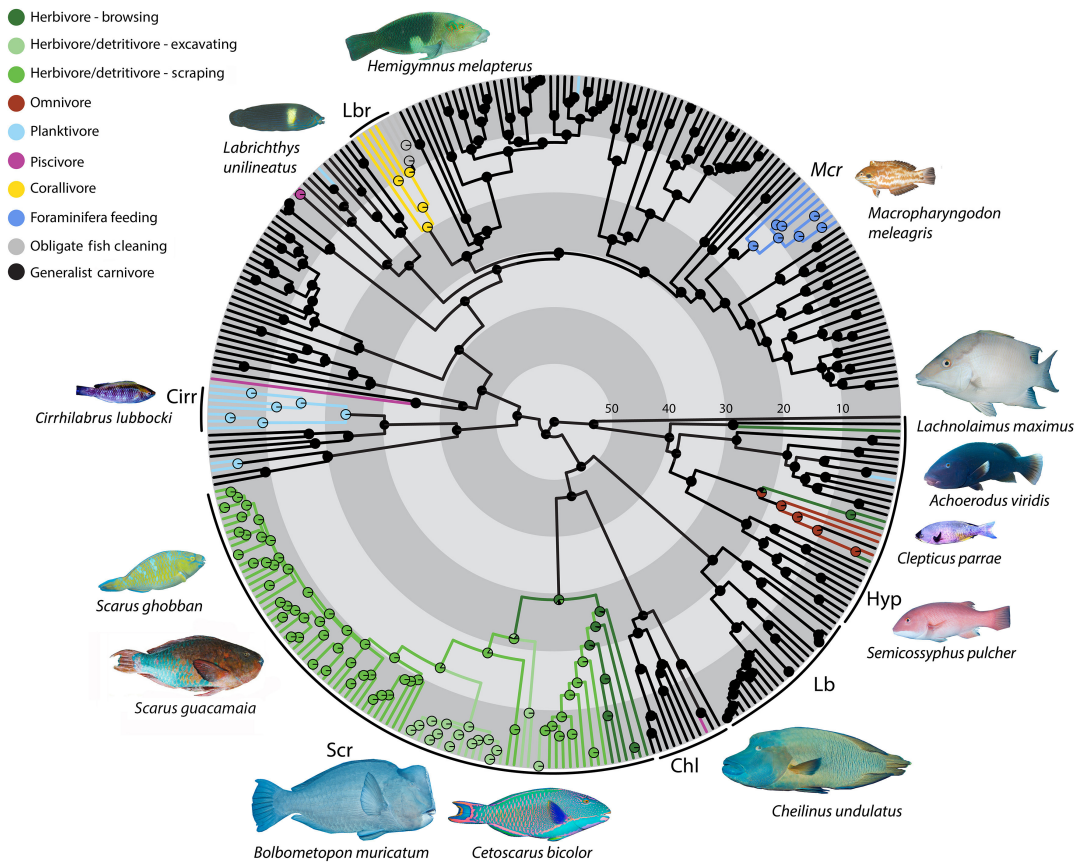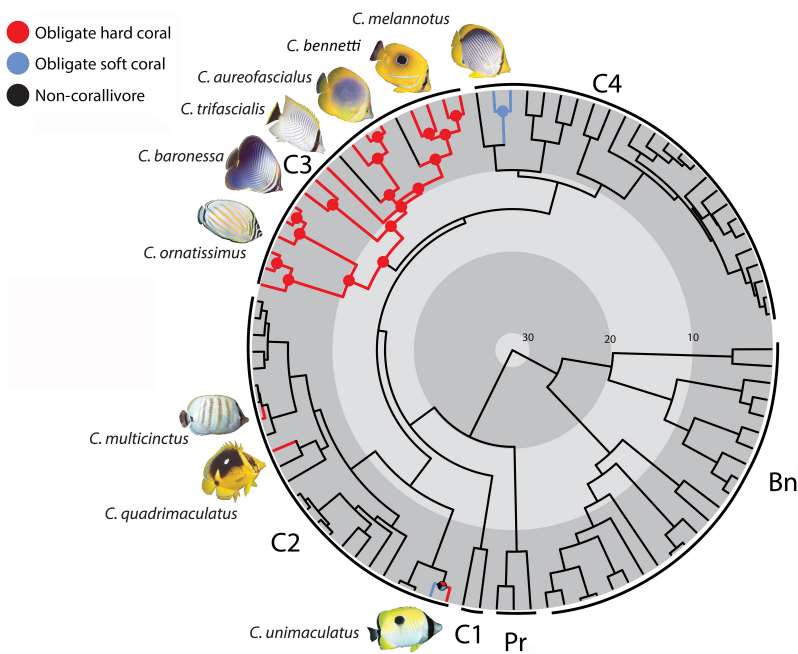1433

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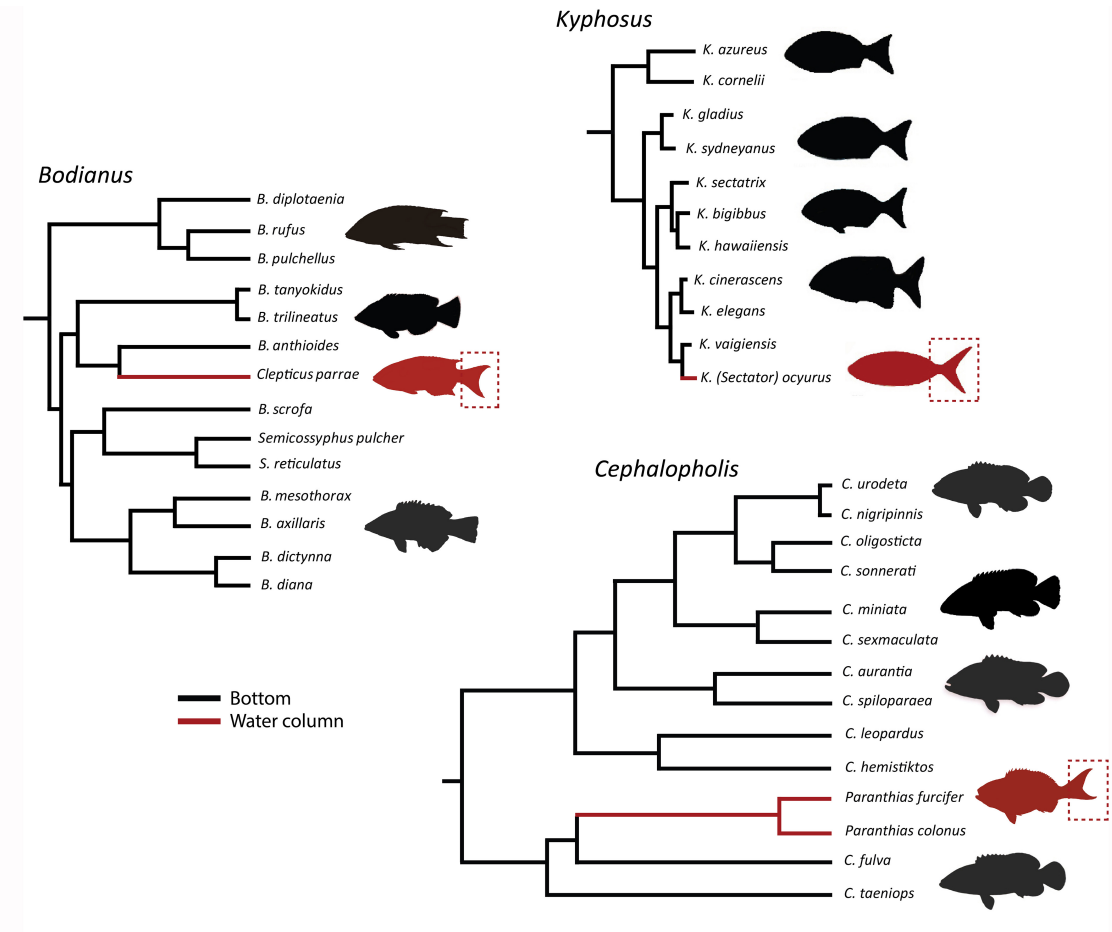1438

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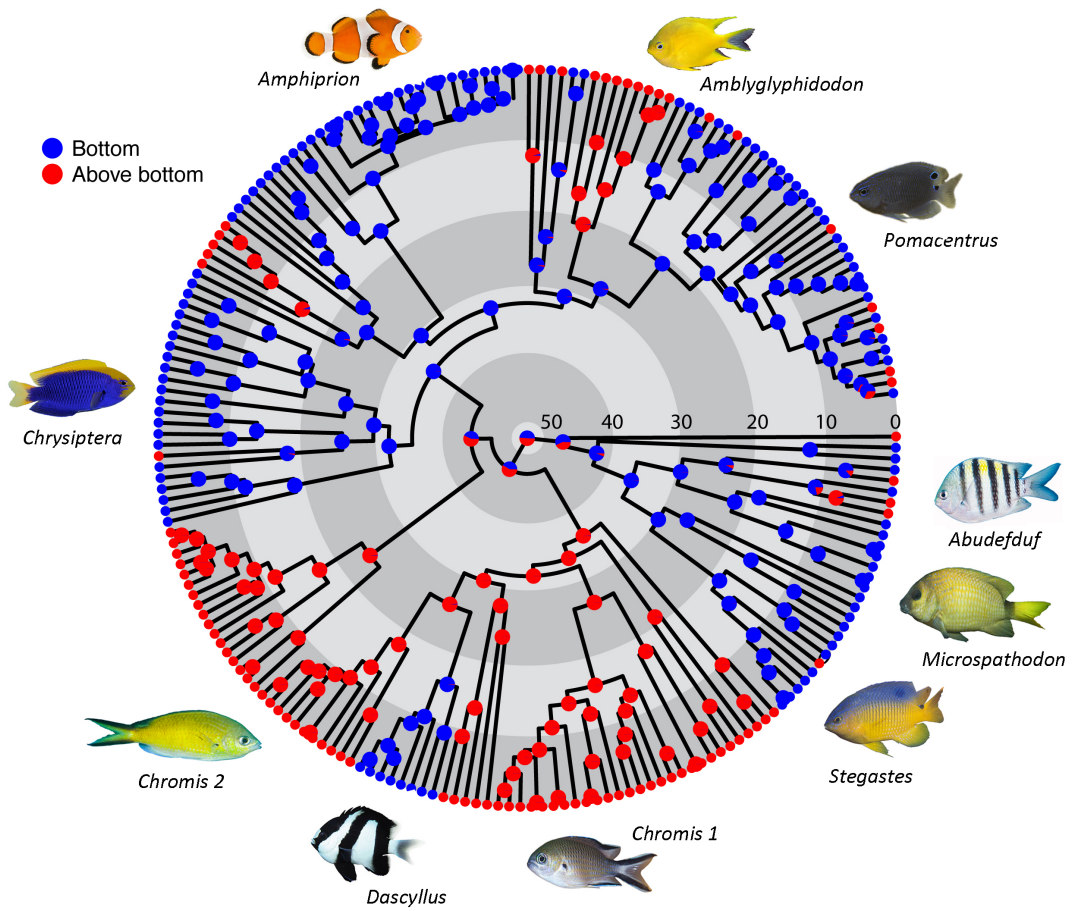

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Figure 3

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Figure 4

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1484   Figure 5

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Log body size
1.5 — 5.4

Hemigymnus melapterus

Halichoeres socialis

Macropharyngodon choati

Lachnolaimus maximus

Cirrhilabrus lubbocki

Semicossyphus pulcher

Scarus ghobban

Choerodon schoenleinii

Scarus guacamaia

Choerodon rubescens

Bolbometopon muricatum

Cetoscarus bicolor

Cheilinus undulatus
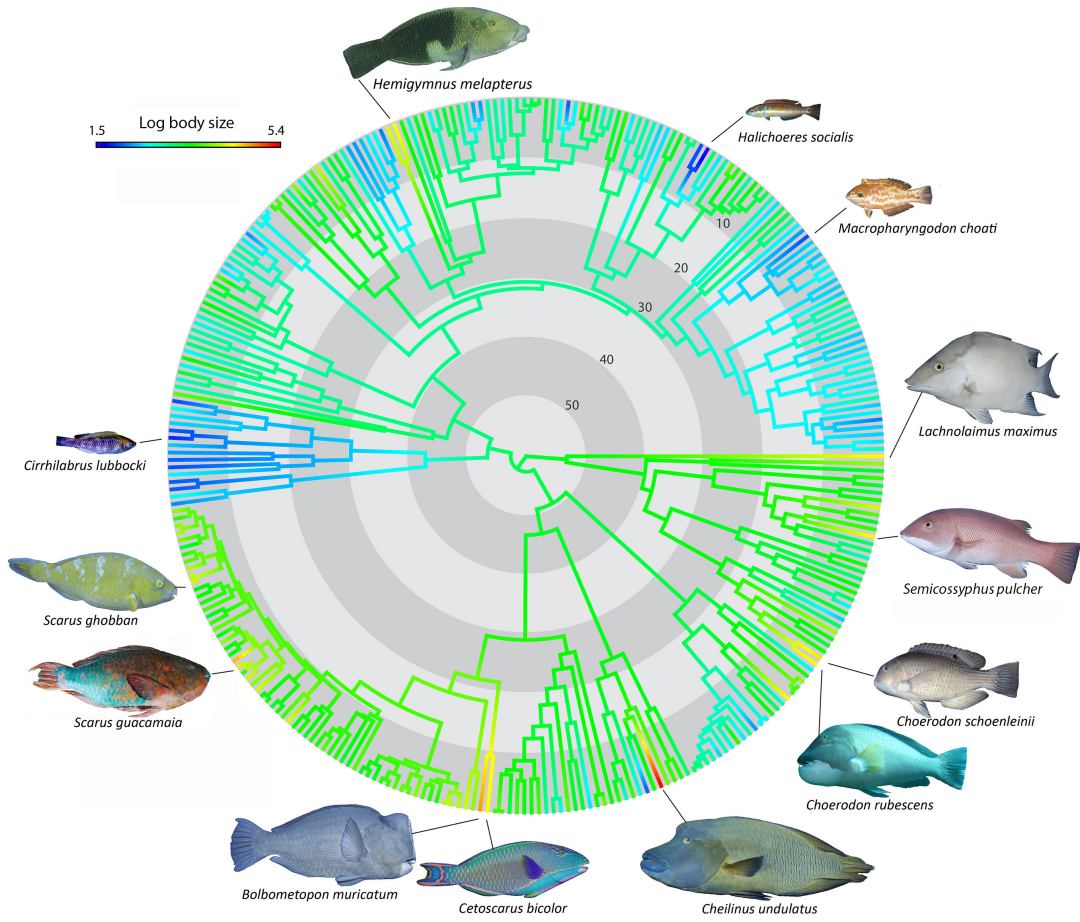
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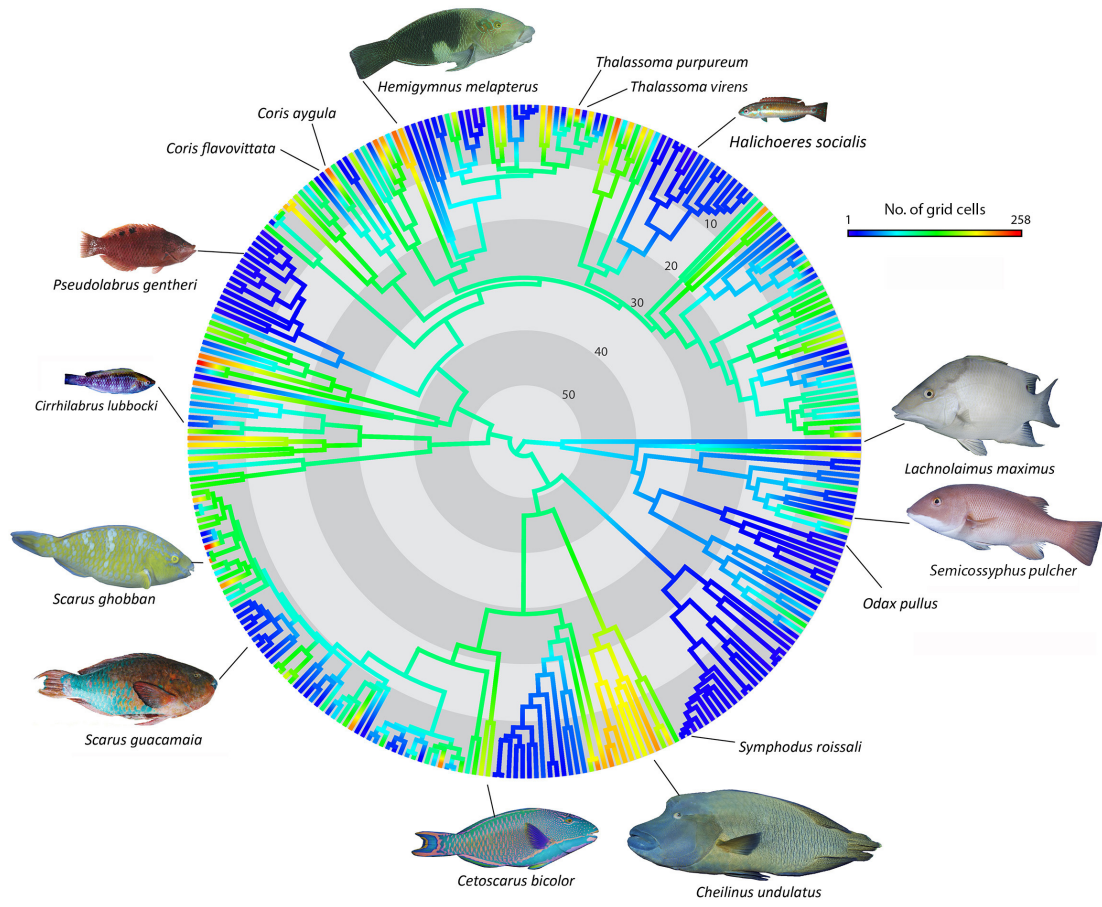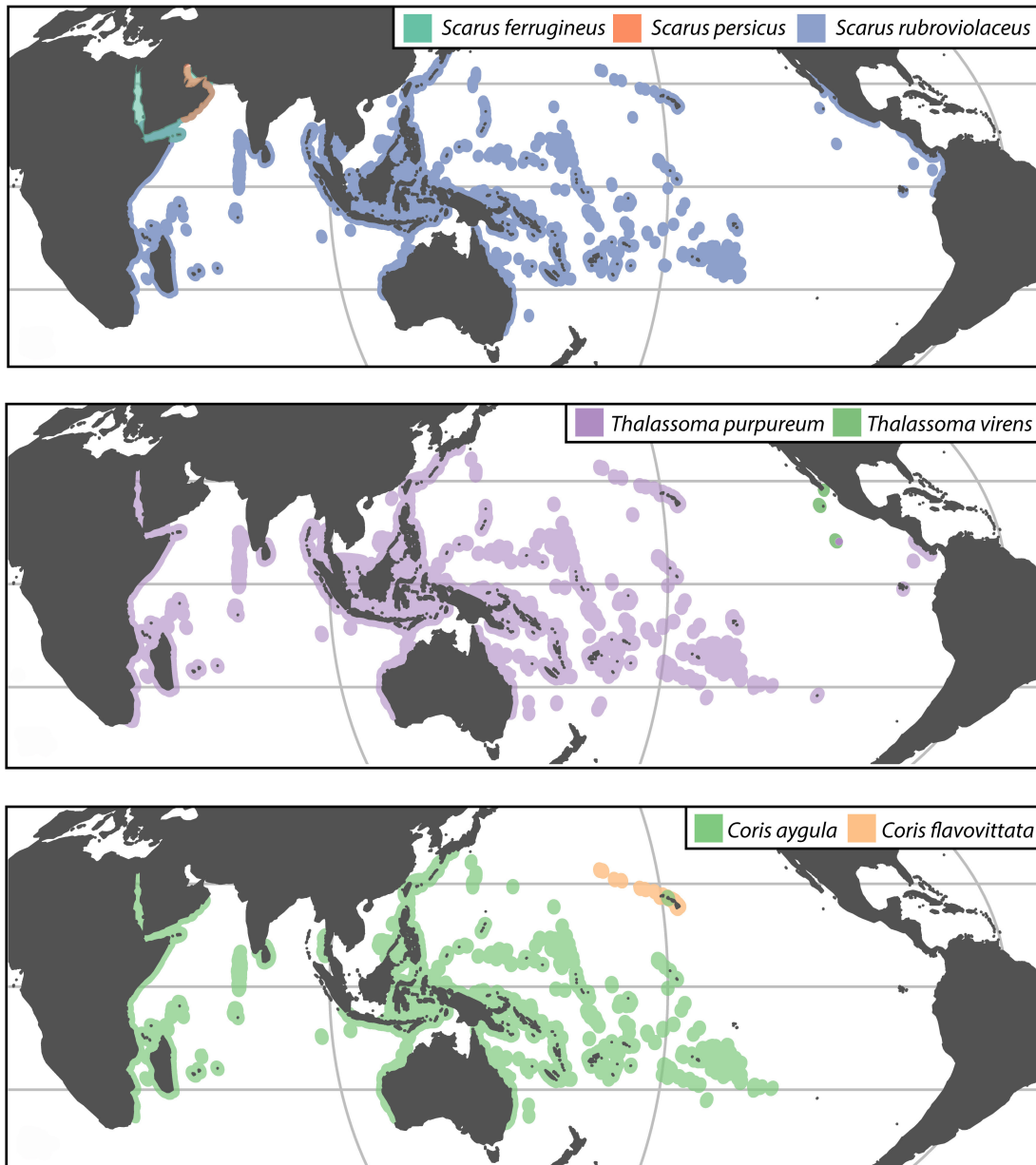
Figure 7

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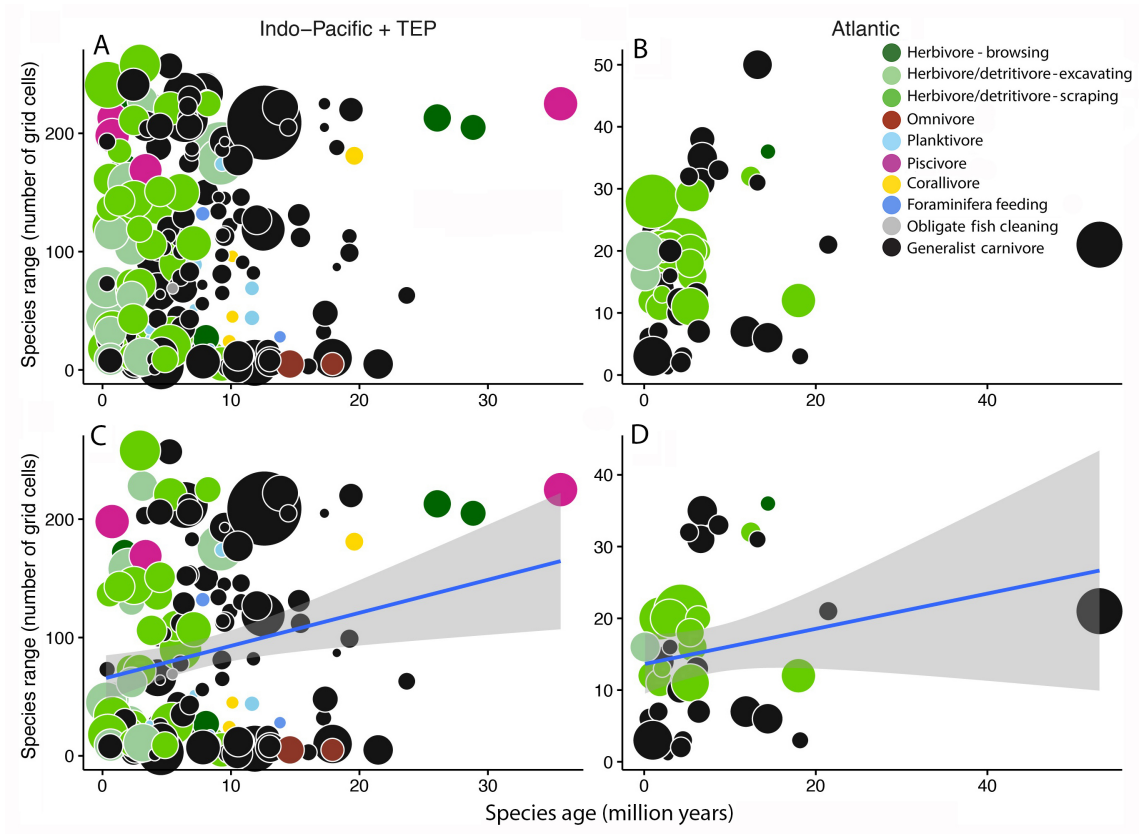
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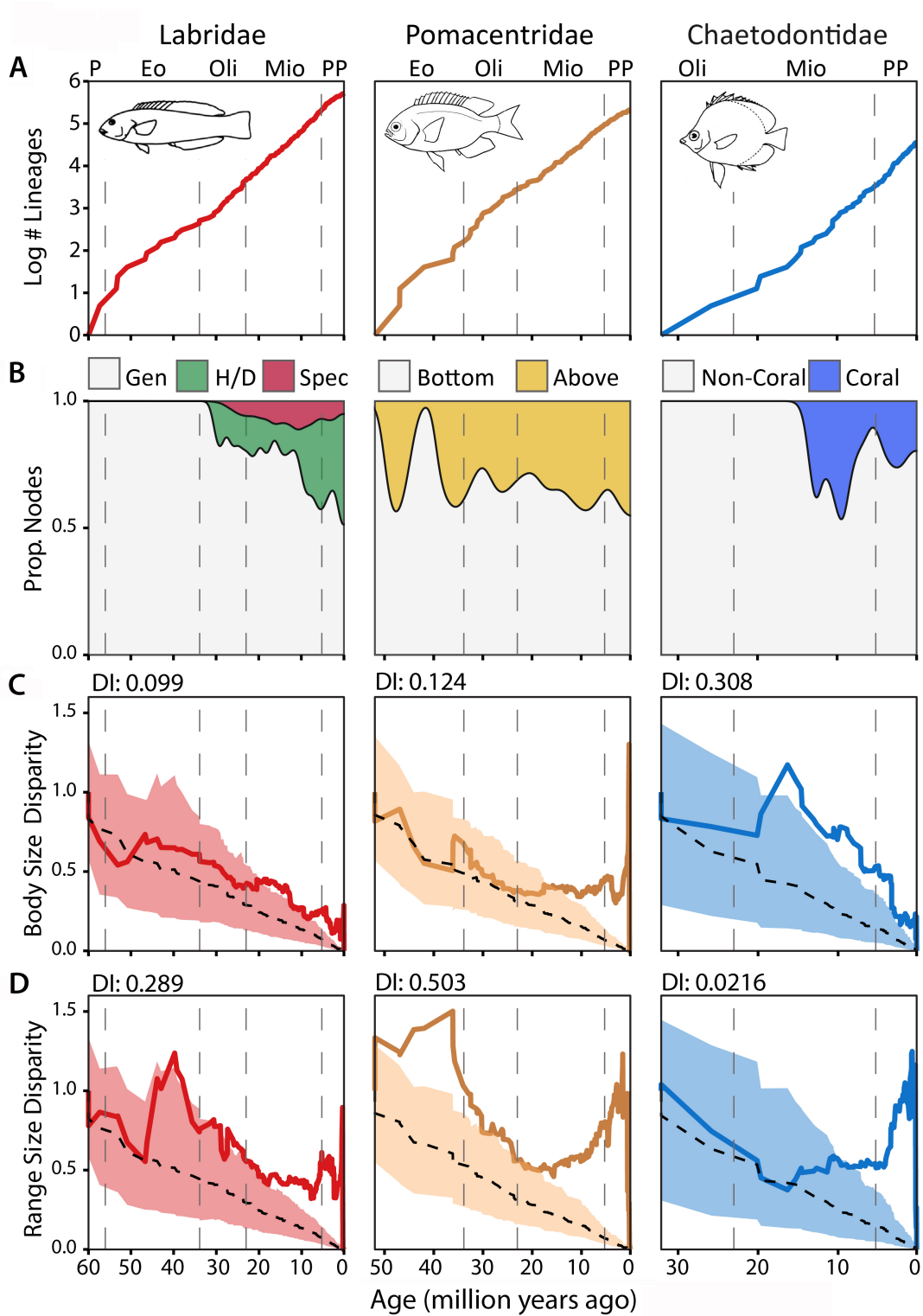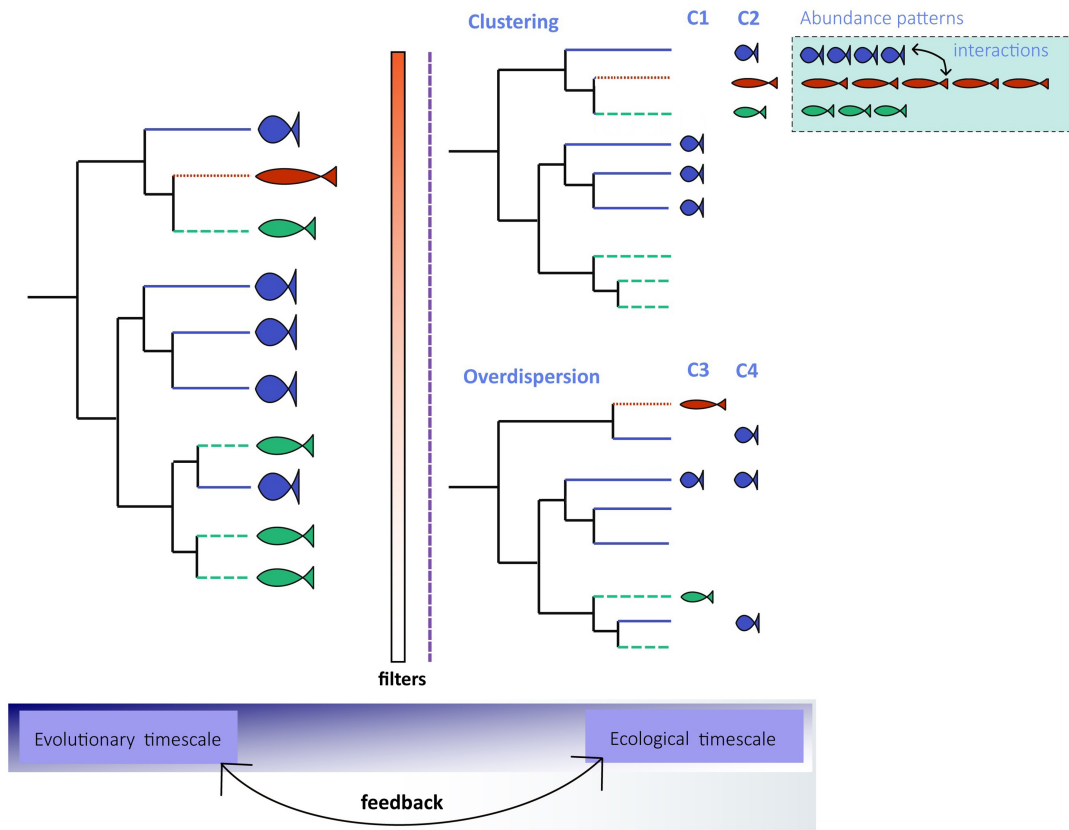1541

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Figure 9

1554   Figure 10

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