

Periodic Environmental Disturbance Drives Repeated Ecomorphological Diversification in an Adaptive Radiation of Antarctic Fishes

Elyse Parker,^{1,*} Katerina L. Zapfe,² Jagriti Yadav,² Bruno Frédérick,³ Christopher D. Jones,⁴ Evan P. Economo,⁵ Sarah Federman,⁶ Thomas J. Near,^{1,7} and Alex Dornburg²

1. Department of Ecology and Evolutionary Biology, Yale University, New Haven, Connecticut 06520; 2. Department of Bioinformatics and Genomics, University of North Carolina, Charlotte, North Carolina 28223; 3. Laboratory of Evolutionary Ecology, Freshwater and Oceanic Science Unit of Research, University of Liège, Liège, Belgium; 4. Antarctic Ecosystem Research Division, National Oceanic and Atmospheric Administration Southwest Fisheries Science Center, La Jolla, California 92037; 5. Biodiversity and Biocomplexity Unit, Okinawa Institute of Science and Technology Graduate University, Okinawa, Japan; 6. Plenty Unlimited, South San Francisco, California 94110; 7. Peabody Museum of Natural History, Yale University, New Haven, Connecticut 06520

Submitted December 6, 2021; Accepted May 5, 2022; Electronically published October 14, 2022

Online enhancements: supplemental PDF.

ABSTRACT: The ecological theory of adaptive radiation has profoundly shaped our conceptualization of the rules that govern diversification. However, while many radiations follow classic early-burst patterns of diversification as they fill ecological space, the longer-term fates of these radiations depend on many factors, such as climatic stability. In systems with periodic disturbances, species-rich clades can contain nested adaptive radiations of subclades with their own distinct diversification histories, and how adaptive radiation theory applies in these cases is less clear. Here, we investigated patterns of ecological and phenotypic diversification within two iterative adaptive radiations of cryonotothenioid fishes in Antarctica's Southern Ocean: crocodile icefishes and notothenichthines. For both clades, we observe evidence of repeated diversification into disparate regions of trait space between closely related taxa and into overlapping regions of trait space between distantly related taxa. We additionally find little evidence that patterns of ecological divergence are correlated with evolution of morphological disparity, suggesting that these axes of divergence may not be tightly linked. Finally, we reveal evidence of repeated convergence in sympatry that suggests niche complementarity. These findings reflect the dynamic history of Antarctic marine habitats and may guide hypotheses of diversification dynamics in environments characterized by periodic disturbance.

Keywords: notothenioid, climate change, morphospace disparity, phylogenomics.

* Corresponding author; email: chantal.parker@yale.edu.

ORCID: Parker, <https://orcid.org/0000-0001-9999-310X>; Zapfe, <https://orcid.org/0000-0002-5159-641X>; Frédérick, <https://orcid.org/0000-0003-3438-0243>; Economo, <https://orcid.org/0000-0001-7402-0432>; Federman, <https://orcid.org/0000-0001-8565-5409>; Near, <https://orcid.org/0000-0002-7398-6670>; Dornburg, <https://orcid.org/0000-0003-0863-2283>.

Introduction

For more than a century, adaptive radiations have provided foundational empirical systems for investigating the factors that promote the diversification of life (e.g., Osborn 1902; Simpson 1944, 1953; Grant 1986; Schluter 2000; Losos 2009). Evolutionary biologists have been particularly interested in understanding the circumstances underlying temporal dynamics of speciation and phenotypic diversification over the course of a radiation. A common expectation holds that adaptive radiations undergo an initial increase in the rates of speciation and phenotypic diversification as new adaptive zones are explored, followed by a decline in diversification rates with increased saturation of adaptive zones and increased specialization of lineages (Simpson 1944, 1953), and this expectation has been supported by numerous empirical studies (e.g., Slater et al. 2010; Arbour and Fernández 2013; Price et al. 2016; García-Navas et al. 2018; Borko et al. 2021). However, some radiating clades have endured complex geophysical and climatic contexts that may have promoted the generation of iterative adaptive radiations of subclades with their own unique diversification histories. For example, many regions of the world have experienced climatic oscillations that significantly affected the biotic and abiotic environments. As environmental changes repeatedly drove some lineages extinct, the freeing of ecological space subsequently provided opportunities for new phases of speciation and diversification (Near et al. 2012; Ivory et al. 2016; Pouchon et al.

2018). While it is natural to expect that such cases could produce evolutionary patterns distinct from a single burst-like adaptive radiation, it is less clear what we should expect in such scenarios. A more nuanced understanding of these iterative adaptive radiations is therefore critical for understanding how extinction and changing environmental conditions shape major components of adaptive radiations following their early evolutionary origins.

The iconic cryonotothenioid fishes of Antarctica's Southern Ocean represent an exemplar clade in which to investigate the factors modulating the shape and pace of an adaptive radiation. Cryonotothenioids comprise nearly 80 phenotypically and ecologically diverse species that dominate the abundance, biomass, and species diversity of the region's nearshore teleost fauna (Eastman 1993, 2005). The remarkable diversification of these fishes has been attributed to periodic cycles of warming and cooling, which have profoundly shaped the physical environment and biodiversity of the Southern Ocean (O'Loughlin et al. 2011; Near et al. 2012; Wilson et al. 2013; Dornburg et al. 2016, 2017). The cyclical advances and retreats of grounded ice across submerged portions of the Antarctic continental shelf (i.e., ice scour) have periodically obliterated benthic nearshore habitat across thousands of kilometers of the Antarctic continental shelf and likely annihilated entire shelf communities (Thatje et al. 2005, 2008; Smale et al. 2008; Tripathi et al. 2009; Allcock and Strugnell 2012; Near et al. 2012; Dornburg et al. 2017). Although laying waste to the incumbent fauna, these ice scour events generate ecological opportunities via the emptying of previously occupied niches. This "resetting of the ecological stage" is thought to have produced a pattern of iterative adaptive radiations nested within the larger cryonotothenioid radiation (Near et al. 2012). The diversification of these subclades likely accounts for the exceptionally rapid speciation rates exhibited by cryonotothenioids relative to other marine teleosts (Rabosky et al. 2018). However, it remains unclear whether and to what extent patterns of phenotypic and ecological divergence within these nested radiations have been impacted by cyclical glacial dynamics.

Most investigations of cryonotothenioid diversification include limited taxon sampling and focus on characterizing patterns across the early radiation. This taxonomically restricted view hinders a detailed understanding of factors that have contributed to iterative adaptive radiations within cryonotothenioids after their early diversification. Recent studies that increased taxonomic sampling revealed that diversification of cryonotothenioids into water column niches spanning the benthic-pelagic axis occurred multiple times in parallel within different cryonotothenioid subclades, suggesting that periodic ice scour disturbances have generated multiple bouts of ecological opportunity for diversification (Rutschmann et al. 2011; Near et al. 2012;

Dornburg et al. 2017). However, to our knowledge, no studies have explicitly examined the relationships among phenotypic and ecological parameters within cryonotothenioid subclades, precluding an understanding of whether aspects of phenotypic and ecological evolution are coupled or whether different lineages have evolved distinct phenotypic strategies to occupy similar niches. Moreover, the extent to which the presence of closely related species that co-occur in a given community influences patterns of trait evolution remains unclear. Investigating the influence of both evolutionary history and potential competitive interactions is critical if we want to understand the diversification history of this adaptive radiation and gain new insights into how biological communities recover in the face of periodic disturbance.

Here, we investigate the patterns of phenotypic and ecological diversification within two cryonotothenioid subclades that have been identified as nested parallel radiations (Near et al. 2012): the crocodile icefishes (Channichthyidae) and the notoperches (Trematominae sensu Near et al. [2018], exclusive of the nested non-Antarctic clade *Patagonotothen*). We compile data on buoyancy, depth occupancy, feeding ecology, body shape and size, and phylogeny to evaluate hypotheses regarding the evolutionary dynamics of ecological and phenotypic trait disparity. We first use phylogenetic least squares regression to evaluate the extent to which the evolution of key phenotypic and ecological traits is correlated. Next, we visualize phylogenetic patterns of trait disparity and use disparity-through-time analyses to evaluate support for alternative expectations of phenotypic and ecological trait diversification within each of our focal radiations. Finally, we test the prediction that interactions among co-occurring species drive elevated trait divergences in adaptive radiation (Dayan and Simberloff 2005; Pfennig and Pfennig 2009). Collectively, our results provide a novel perspective on the patterns of ecomorphological diversification within the cryonotothenioid adaptive radiation.

Methods

Trait Data Collection

We compiled data on a series of traits that are hypothesized as central to the adaptive radiation of cryonotothenioids: mean percentage buoyancy, which functions as a proxy for water column niche (Near et al. 2012; Eastman 2017); depths of occurrence (table S1); frequency of occurrence of prey items (figs. S1, S2; table S2); geometric morphometric data on body shape (fig. S3; table S3); and maximum body size (table S4), represented using the maximum total length (TL) recorded for each species (Matschner et al. 2011; Near et al. 2012; Colombo et al. 2015; Dornburg et al. 2017; Eastman 2017, 2019, 2020; Daane et al. 2019).

Before conducting downstream analyses of trait diversification patterns, we identified major axes of variation in diet using a phylogenetic principal components analysis (PCA) of the prey frequency occurrence data using the R package *phytools* (Revell 2011). Additionally, the geometric morphometric data on body shape were first transformed using a generalized Procrustes analysis (GPA; Rohlf and Slice 1990; Zelditch et al. 2012) and then subjected to a phylogenetic PCA in the R package *geomorph* (Adams et al. 2021; Baken et al. 2021). Full details of the trait data collection are provided in “Supplementary Methods” in the supplemental PDF. All data have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.bk3j9kdbg>; Parker et al. 2022).

Divergence Time Estimation

To estimate a time-calibrated phylogeny of cryonotothenioids for comparative analyses, DNA alignments were taken from Near et al. (2018), who used restriction site-associated DNA sequencing to capture 104,709 loci across 80 species of notothenioids. Divergence times were estimated using BEAST (ver. 2.4.7; Drummond et al. 2012; Drummond and Bouckaert 2015) assuming an uncorrelated model of molecular rates with a lognormal distribution and a birth-death prior on branching times. We placed four prior age constraints used in previous studies of notothenioid divergence times (see “Supplementary Methods” in the supplemental PDF; Near et al. 2012; Dornburg et al. 2017). Adequate sampling of the posterior distribution for each parameter of each run was assessed via computation of effective sample size (ESS) values, with ESS values >200 indicating adequate sampling. Marginal posterior probabilities versus generation state were assessed for each parameter in the program Tracer (ver. 1.6; <http://beast.bio.ed.ac.uk/Tracer>). A maximum clade credibility (MCC) tree was generated using TreeAnnotator (ver. 2.4.7; <http://beast.bio.ed.ac.uk/TreeAnnotator>) to summarize the posterior probability density of topological and branch-length estimates. For downstream phylogenetic comparative analyses, we extracted from the MCC tree one subtree including all 14 species representing the crocodile icefishes and one subtree including all 16 species representing the notoperches (fig. S4). Full details of our phylogenetic analyses can be found in “Supplementary Methods” in the supplemental PDF.

Testing for Evidence of Correlated Evolution

To investigate potential evolutionary correlations among body shape and major axes of ecological disparity in icefishes and notoperches, we performed multivariate phylo-

genetic generalized least squares (PGLS) regression using the *procD.pgls* function in the R package *geomorph* (Adams et al. 2021; Baken et al. 2021). This approach enabled us to test the relationships between morphology and ecology while accounting for the expected covariance of traits among species due to shared ancestry. In each of our tests, body shape variation was the response variable and was represented using the full set of species-averaged Procrustes shape coordinates from the GPA. We first tested whether changes in body size (represented by maximum TL) are associated with predictable changes in body shape. We then assessed relationships between changes in body shape and changes in habitat and prey usage by conducting a series of regressions of body shape on mean percentage buoyancy, mean depth occupancy, and each of the first three PC axes of diet variation from PCA of the prey frequency occurrence data.

To test whether changes in ecology predict changes in only the major axes of body shape variation, we fitted a series of linear regression models in which each of the first three PC axes of body shape variation from a PCA of the Procrustes shape coordinates was used as the response variable and each of the ecological variables (including mean percentage buoyancy, mean depth, and each of the first three PC axes of diet variation) was used as the predictor variable. We additionally tested whether changes in body size predict changes along each of the first three PC axes of body shape variation as well as whether changes in our ecological variables predict changes in body size. Furthermore, we assessed relationships among each of the ecological variables used to represent habitat and prey usage for icefishes and notoperches. We first tested whether mean percentage buoyancy and mean depth are correlated, given that both traits represent major axes of variation in habitat utilization in cryonotothenioids (Eastman 2017, 2020). We then evaluated whether changes in habitat utilization (represented using either mean percentage buoyancy or mean depth) are associated with predictable changes in prey usage (represented by the first three PC axes of diet variation). For all of these tests, we used the *gls* function in the *nlme* R package (Pinheiro et al. 2017) to fit linear models of trait correlation in which the covariance structure was defined according to either a Brownian motion model or a Ornstein-Uhlenbeck model of trait evolution on each clade’s phylogeny (specified using either the *corBrownian* function or the *corMartins* function, respectively, in the *ape* R package; Paradis et al. 2004). Across all tests of correlated evolution, tests were performed independently for icefishes and for notoperches, and *r* and *P* values were adjusted using the false discovery rate correction method of Benjamini and Hochberg (1995) implemented using the *p.adjust* R function.

*Visualizing Evolutionary Dynamics
of Trait Diversification*

We used a series of visualizations to qualitatively evaluate the diversification history of each trait in this study. First, patterns of divergence in bathymetric distribution were visualized using ridgeline plots (Fitzpatrick et al. 2019) in proximity to each clade's time tree. This approach allowed us to directly contrast the range of the water depths occupied by each lineage. We then assessed divergences along major axes of variation in diet by generating phenograms, which project a phylogeny into trait space defined by each of the first three PC axes of variation in prey usage. Phenograms were also used to visually assess variation in body size as well as patterns of morphospace occupancy, where each of the first three axes of body shape variation from the PCA were plotted along with the phylogeny of each clade. All phenograms were generated using the R package *phytools* (Revell 2011).

In addition to visualizing phylogenetic patterns of trait disparity, we used the R package *geiger* (ver. 2.0; Pennell et al. 2014) to calculate relative subclade disparity through time (DTT; Harmon et al. 2003) for mean percentage buoyancy, mean depth, and maximum body size. This approach allowed us to test the competing expectations that historical patterns of adaptive radiation have left a signature of among-subclade disparity in the early history of these clades versus an expectation of high within-clade disparity driven by convergence. We restricted our analyses to these traits, as ordination analyses have the potential to bias major axes of variation toward patterns consistent with early-burst models (Uyeda et al. 2015). We compared the empirical DTT results with the expectations of a null model of Brownian motion generated from 10,000 simulations (Slater et al. 2010).

*Testing the Relationships between Range Overlap,
Clade Age, and Ecomorphological Diversification*

Interactions between species living in sympatry are thought to promote increased divergence in ecological traits (Pfennig and Pfennig 2009; Tobias et al. 2014). Alternatively, elevated trait divergences may reflect greater evolutionary time since two species shared a common ancestor. To test whether levels of ecomorphological divergence among icefishes and notoperches can be predicted by range overlap (a proxy for interspecific interactions) or time since common ancestry, we fitted a series of phylogenetic generalized linear mixed models (PGLMMs) using the R package *MCMCglmm* (Hadfield 2010). In each model, our response variable corresponded to divergence in a given ecological or phenotypic trait for all possible pairwise comparisons of species within each of the icefish and notoperch clades.

We used the *dist* function in R to calculate pairwise divergence as the Euclidean distance between species in mean percentage buoyancy, mean depth, maximum TL, and PC scores for each of the first three PC axes of variation in diet and in body shape. We tested the effects of three fixed predictors on ecomorphological divergence: (1) the range overlap for a given species pair (modeled as a two-level factor: sympatric, allopatric), (2) the time since common ancestry (millions of years) for a given species pair, and (3) the interaction between range overlap and time since common ancestry. Our models additionally accounted for two random effects: (1) the nonindependence of trait values arising from shared ancestry of lineages and (2) the nonindependence of data points arising from repeated measurements of each lineage (Tobias et al. 2014). We accounted for phylogenetic nonindependence by fitting as a random effect the variance-covariance (VCV) matrix calculated from each clade's MCC tree and connecting the VCV matrix to data points via the most recent common ancestral node shared by a given species pair. Nonindependence arising from repeated measurements was accounted for by fitting species identifiers (as either the focal lineage or the comparison lineage in each pairwise comparison) as random effects.

Model fitting was conducted independently for notoperches and for icefishes, and we fitted separate linear mixed models for each trait. Inverse gamma priors were applied to the variance structure of the random effects. For all models, the posterior distributions of model parameters were simulated using 20 million Markov chain Monte Carlo generations, with sampling every 10,000 generations after discarding the first 10% of generations as burn-in. Model convergence was assessed by visualizing trace plots for each of the estimated parameters in each model and by ensuring that ESS values exceeded 200 for each parameter estimate. Full details of these analyses can be found in "Supplementary Methods" in the supplemental PDF.

Results

Correlated Evolution

Results of our PGLS regressions revealed no evidence that body size or any of the major axes of diet variation strongly influence variation in the Procrustes body shape coordinates across icefishes ($P > .05$ for all regressions; table S5) or notoperches ($P > .05$ for all regressions; table S6). Similarly, for both icefishes and notoperches, our PGLS regressions reveal no evidence that divergences along any of the major PC axes of body shape variation are correlated with divergences in diet, depth occupancy, or percentage buoyancy ($P > .05$ for all regressions; tables S7–S10). We additionally find no evidence that changes in diet, depth occupancy, or buoyancy are associated with predictable

changes in maximum body size ($P > .05$; tables S7–S10). Finally, our results do not uncover significant relationships among any of the major ecological axes of divergence in the icefish and notoperch radiations. Specifically, variation in prey usage is not predicted by either depth occupancy or habitat use along the benthic-pelagic axis ($P > .05$), and divergence along the benthic-pelagic axis does not predict divergence in depth occupancy ($P > .05$; tables S7–S10).

Diversification of Feeding Ecology

The first three PC axes explained approximately 95% of the variation in icefish diet (fig. S5). PC1 (66%) captured variation largely between the consumption of cephalopods and krill (fig. S5). PC2 (24%) and PC3 (5%) similarly reflected changes in the consumption of krill, cephalopods, and fishes, with PC3 further including differences in the consumption of munids (fig. S5). Projecting the phylogeny into trait spaces defined by each of these three PC axes reveals striking patterns of convergence in feeding ecology between distantly related lineages (fig. 1A–1C). For example, *Dacodraco hunteri*, *Chionodraco hamatus*, *Chionodraco myersi*, and *Channichthys rhinoceratus* all converge on a nearly identical point in the trait space defined by the first PC axis of diet variation, reflecting a convergence on piscivory (fig. 1A). Similarly, *Pagetopsis maculatus* and *Chaenodraco wilsoni* converge on a point in the space defined by the second PC axis of diet, reflecting increased krill consumption (fig. 1B). In contrast, closely related species and sister species pairs often appear highly divergent along any of the first three PC axes. Examples include the divergences between *Champscephalus esox* and *Champscephalus gunnari*, *C. wilsoni* and *C. myersi*, and *Chionobathyscus dewitti* and *Cryodraco antarcticus* (fig. 1A–1C).

In notoperches, the first three PC axes explain 70% of the variation. PC1 (38%) captured variation largely in consumption of *Hyperiella*, copepods, and polychaetes (fig. S6). PC2 (19%) and PC3 (13%) similarly show variation in marine invertebrate prey, including amphipods (fig. S6). Similarly to icefishes, projections of the phylogeny into trait spaces defined by each of the first three PC axes of diet variation reveal patterns of convergence in feeding ecology between distantly related species (fig. 1D–1F). For example, in the diet space generated by PC1, distant lineages *Trematomus loennbergii* and *Trematomus scotti* converge on polychaete consumption (fig. 1D), and in the diet space generated by PC2, *Nototheniops cf. nudifrons*, *Trematomus eulepidotus*, and *Trematomus newnesi* all converge on a space between copepods and euphausiids (fig. 1E). Furthermore, the first three PC axes show recently diverged notoperch lineages diverging in diet space, including between the sister pair *T. loennbergii* and *T. lepidorhinus*

and between their common ancestor and *T. eulepidotus* (fig. 1D–1F).

Diversification in the Water Column

Our visualizations of depth distributions for icefishes reveal a complex pattern of evolutionary changes in water column usage, with several cases of closely related species partitioning the water column (fig. 2). For example, *C. myersi* (quartiles: 25% = 398 m, 50% = 430 m, 75% = 439 m) has shifted its water column usage by over 200 m from the closely related *C. wilsoni* (quartiles: 25% = 231 m, 50% = 257 m, 75% = 353 m; table S1). Similarly, *C. antarcticus* is encountered primarily near 350 m (quartiles: 25% = 326 m, 50% = 364 m, 75% = 423 m), while *C. dewitti* occupies depths closer to 400 m (quartiles: 25% = 367.25 m, 50% = 390 m, 75% = 411.5 m; table S1). In notoperches, the contrasts between closely related species are more striking. In no case does the bulk of the depth distribution overlap between closely related pairs of species (fig. 3). These changes largely reflect a partitioning of the water column by 100–200 m between closely related species such as *Trematomus nicolai* (quartiles: 25% = 248.5 m, 50% = 403 m, 75% = 458.5 m) and *Trematomus pennellii* (quartiles: 25% = 169 m, 50% = 208 m, 75% = 231 m; table S1). However, some cases are more extreme, such as the contrast between *T. eulepidotus* (quartiles: 25% = 242 m, 50% = 320 m, 75% = 408 m) and *T. loennbergii* (quartiles: 25% = 574.75 m, 50% = 754.5 m, 75% = 759 m; table S1).

Major Axes of Body Shape Evolution

The first three PC axes explained approximately 68% of body shape variation in icefish (fig. S7A). PC1 (accounting for 37% of variance) is primarily associated with variation in body depth, PC2 (19% of variance) corresponds to variation in mouth position, and PC3 (12% of variance) captures variation in snout length (figs. 4A–4C, S7A). Our phenograms reveal several instances of convergence of distantly related icefish species in aspects of body shape. For instance, *C. antarcticus*, *C. esox*, and *C. gunnari* converge on a relatively slender, elongate body shape, while *Pseudochaenichthys georgianus* and *Pagetopsis macropterus* converge on deeper-bodied forms (fig. 4A–4C). However, examination of the first three PC axes also reveals striking divergences in aspects of body shape among closely related species, including sister species pairs *P. macropterus* and *P. maculatus*, *C. antarcticus* and *C. dewitti*, and *C. hamatus* and *C. rastrispinosus* (fig. 4A–4C).

In notoperches, the first three PC axes explain 62% of the variance in body shape (fig. S7B). PC1 (39% of variance)

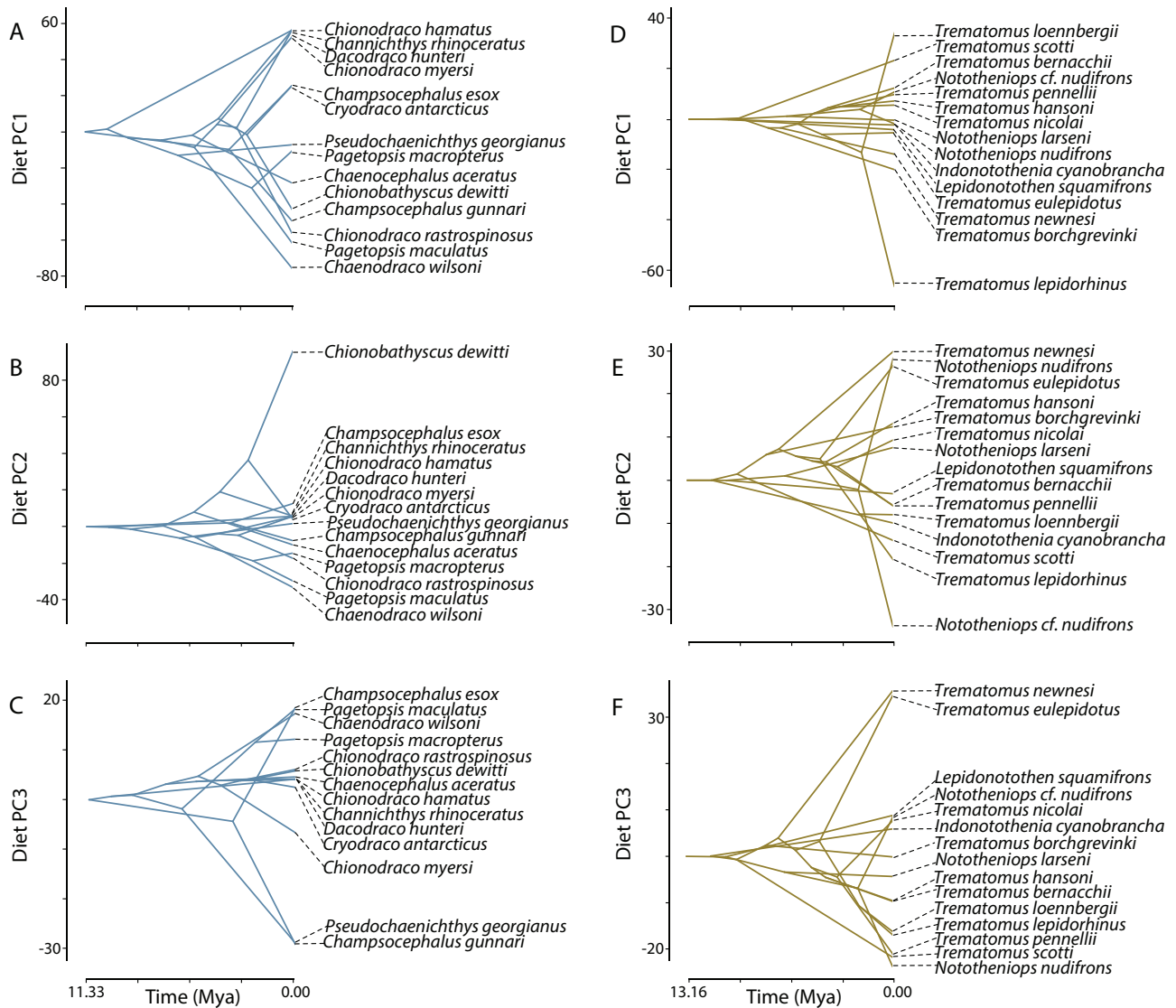


Figure 1: Evolutionary histories of the top three principal component (PC) axes of diet variation reveal complex patterns of repeated convergence in prey usage among distantly related species and high divergence among closely related species. A–C represent projections of the crocodile icefish phylogeny, and D–F represent projections of the notoperch phylogeny. In all panels, the x-axis represents time in millions of years, with branch lengths reflecting estimated divergence times. The y-axis reflects variation along each of the first three PC axes of diet, with tip placement along the y-axis reflecting the PC score for that species along each PC axis.

is primarily associated with variation in mouth position, PC2 (16%) corresponds to variation in head depth and body depth at anal fin origin, and PC3 (7%) describes variation in caudal peduncle length (figs. 4D–4F, S7B). Similar to our observations for icefishes, we observe multiple instances of trait convergence among distantly related notoperch species. For instance, *Nototheniops larseni* and *T. lepidorhinus* converge on a relatively upturned mouth position, and *T. newnesi*, *T. nicolai*, and *T. bernacchii* all converge on a relatively slender, elongate body shape (fig. 4D–4F). Meanwhile, we

find evidence of high divergence in body shape among closely related species, as exemplified by the pairs *T. lepidorhinus* and *T. loennbergii*, *T. pennellii* and *T. nicolai*, and *T. bernacchii* and *T. hansonii* (fig. 4D–4F).

Body Size Variation

Similar to patterns of disparity in diet, habitat utilization, and body shape, we observe complex patterns of evolutionary

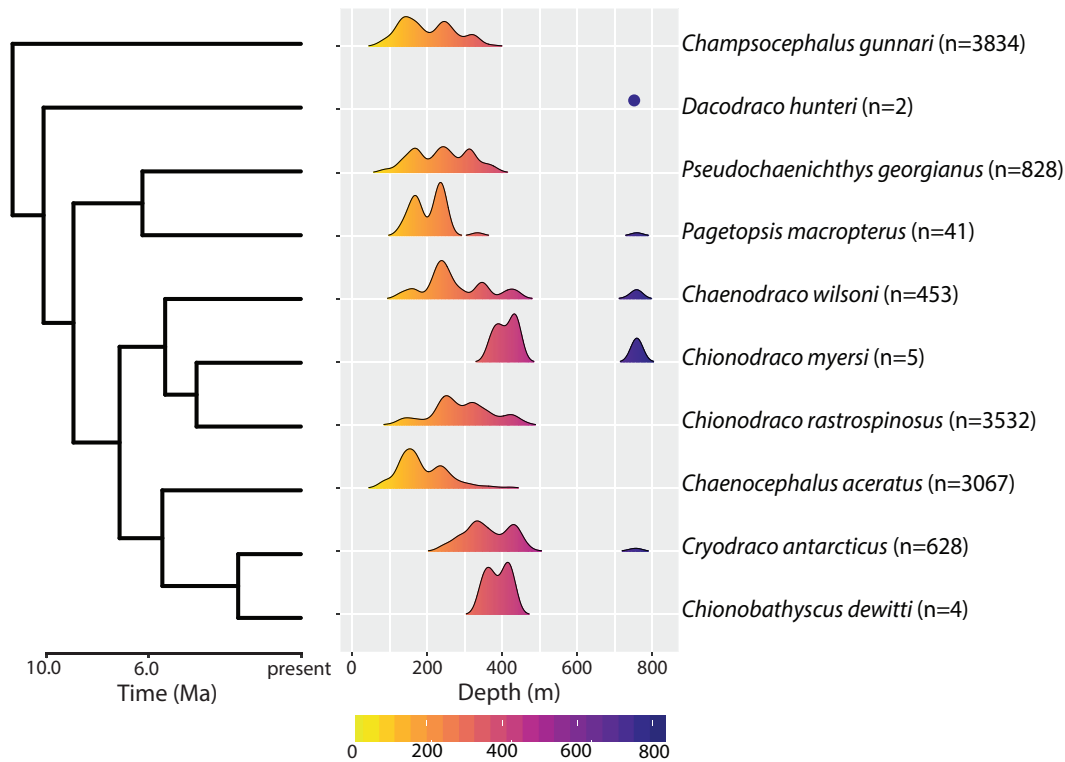


Figure 2: Depth partitioning among closely related icefish species in a phylogenetic framework. *Left*, time-calibrated phylogeny of notoperches, with branch lengths reflecting estimated divergence times (millions of years ago). *Right*, ridgeline plots depict the relative density of all capture depths (m) for each species from 12,395 recorded encounters in trawl data. Shading of densities indicates depth of capture. Depth axis of each ridgeline plot corresponds to the adjacent tip in the phylogeny. Sample sizes (n) are given to the right of each species name.

convergence and divergence in body size among icefishes and notoperches. Within icefishes, distantly related species *D. hunteri* and the *P. macropterus*–*P. maculatus* species pair converge on relatively small maximum body sizes (25–33 cm), while *C. gunnari* (68 cm) and *Chaenocephalus aceratus* (76 cm) converge on maximum body sizes approximately two times greater than those recorded for the smallest icefish species (fig. 5B). High divergence in body size is also obvious between closely related species, such as between *C. gunnari* (68 cm) and *C. esox* (35 cm) and between *P. georgianus* (60 cm) and *P. maculatus* (25 cm; fig. 5B). In notoperches, we find several closely related species to exhibit high divergence in body sizes, including *T. hansonii* (45.5 cm) and *T. tokarevi* (22.4 cm; fig. 5A). We also observe several instances of convergence among distantly related species of *Trematomus*, *Notototheniops*, and *Lepidonotothen*. For example, *T. hansonii* and *Lepidonotothen squamifrons* converge on relatively large maximum body sizes compared with all other notoperches (45.5 cm and 54 cm, respectively; fig. 5A), while *T. scotti* exhibits convergence with *N. nudifrons* and *N. cf. nudifrons* on a maximum reported body size of ~19 cm (fig. 5A).

Patterns of Disparity through Time

Analyses of the average relative subclade disparity through time (DTT) provide little general support for an early partitioning of the overall disparity among subclades (fig. 6). High variance across Brownian motion simulations probably results from small clade sizes and limits the power to statistically reject one hypothesis over the other (fig. 6). However, the trends revealed by DTT plots mirror the ones depicted in trait phenograms (figs. 1, 4, 5). Analysis of buoyancy disparity through time reveals levels of relative subclade disparity that are higher than the mean trend of DTT expected for icefishes (morphological disparity index [MDI] = 0.30, $P = .90$; fig. 6A), running counter to the trend for depth (MDI = -0.18 , $P = .083$; fig. 6B). The latter represents the only case of early low relative subclade disparity and contrasts sharply with body size DTT, which depicts a signature of within-clade disparity consistent with high levels of between-clade trait convergence (MDI = 0.36, $P = .92$; fig. 6C). Notoperches similarly reveal trends more consistent with convergent evolution in buoyancy (MDI = -0.037 , $P = .32$; fig. 6D) and depth

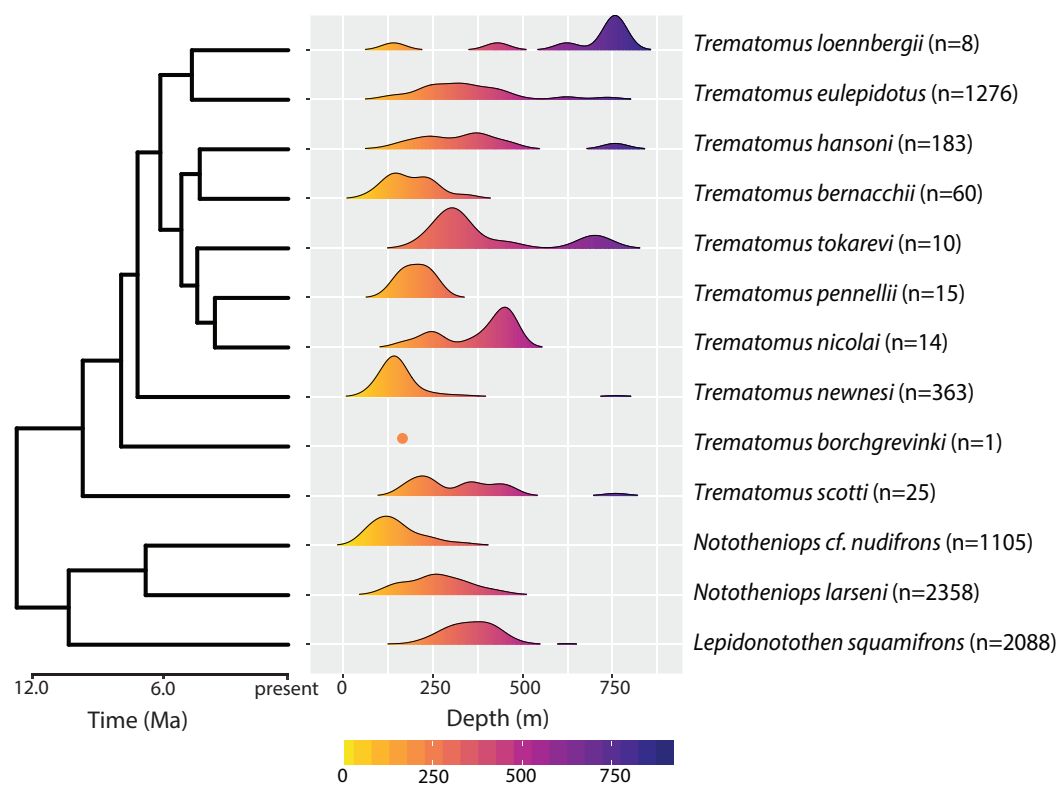


Figure 3: Depth partitioning among closely related noto-perch species in a phylogenetic framework. *Left*, time-calibrated phylogeny of noto-perches, with branch lengths reflecting estimated divergence times (millions of years ago). *Right*, ridgeline plots depict the relative density of all capture depths (m) for each species from 7,532 recorded encounters in trawl data. Shading of densities indicates depth of capture. Depth axis of each ridgeline plot corresponds to the adjacent tip in the phylogeny. Sample sizes (n) are given to the right of each species name.

(MDI = 0.25, $P = .79$; fig. 6E) during their evolutionary history. Likewise, the evolution of body size disparity reflects a signal of high levels of convergence in body size between clades rather than a partitioning of body size diversity between clades (MDI = -0.018 , $P = .41$; fig. 6F).

The Relationships between Range Overlap, Clade Age, and Ecomorphological Diversification

For all pairwise comparisons of lineages within icefishes and noto-perches, we generally find that range overlap, clade age, and the interaction between range overlap and clade age do not significantly predict observed levels of ecological or phenotypic divergence (table S11, pts. a–g; table S12, pts. a–i). However, within noto-perches, patterns of divergence in several traits exhibit exceptions to this general finding. First, our PGLMMs reveal that pairwise divergences in the third PC axis of body shape variation (table S12, pt. e) and in body size (table S12, pt. i) are higher across sympatric species pairs relative to allopatric species pairs. Second, we find evidence for significant positive relationships between clade age and divergence in

buoyancy (table S12, pt. a), depth occupancy (table S12, pt. b), and body size (table S12, pt. i). Finally, we find a significant negative relationship between divergence in depth and the interaction between range overlap and clade age (table S12, pt. b).

Discussion

Here, we integrated a strongly supported species-level phylogenetic hypothesis with a comprehensive data set on body shape and size, diet, depth, and buoyancy to elucidate patterns of ecomorphological diversification within two cryonotothenioid subclades that have been identified as iterative adaptive radiations: the crocodile icefishes and the noto-perches. Our results reveal several unique patterns of adaptive radiation that have likely been influenced by the high-frequency disturbance regime characteristic of Antarctica's continental shelf. First, we find limited evidence that changes in body shape and size are correlated with divergences along axes of habitat and prey usage. Second, we primarily observe high dissimilarity between closely

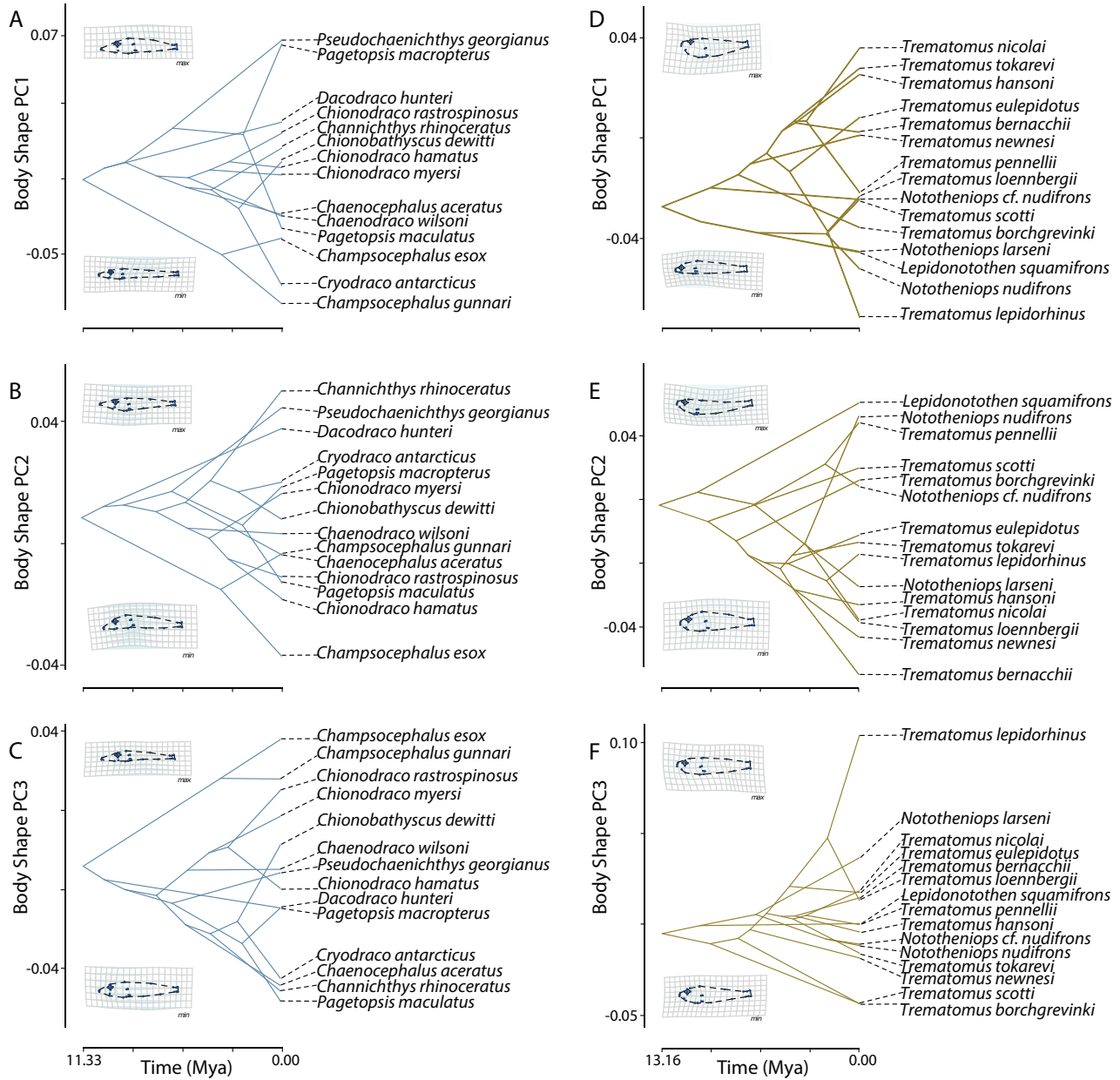


Figure 4: Evolutionary histories of the top three principal component (PC) axes of body shape variation demonstrate several instances of convergence of distantly related species in aspects of body shape as well as striking divergences among closely related species. A–C represent projections of the crocodile icefish phylogeny, and D–F represent projections of the noto-perch phylogeny. In all panels, the x-axis represents time in millions of years, with branch lengths reflecting estimated divergence times. The y-axis reflects variation along each of the first three PC axes of body shape, with tip placement along the y-axis reflecting the PC score for that species along each PC axis.

related species and repeated convergences among distantly related species in trait space, suggesting repeated trait diversification in both the crocodile icefish and noto-perch radiations. Finally, we find only limited support for elevated diversification between sympatric species pairs. Instead, across each of our focal traits, we observe repeated convergence of sympatric species into overlapping regions

of trait space, a pattern that is likely maintained by niche complementarity. Our findings are consistent with a scenario in which periodic environmental disturbances provided recurrent generation of ecological opportunities for diversification, thereby guiding the development of hypotheses of trait diversification in other environments characterized by a history of climate instability or heterogeneity.

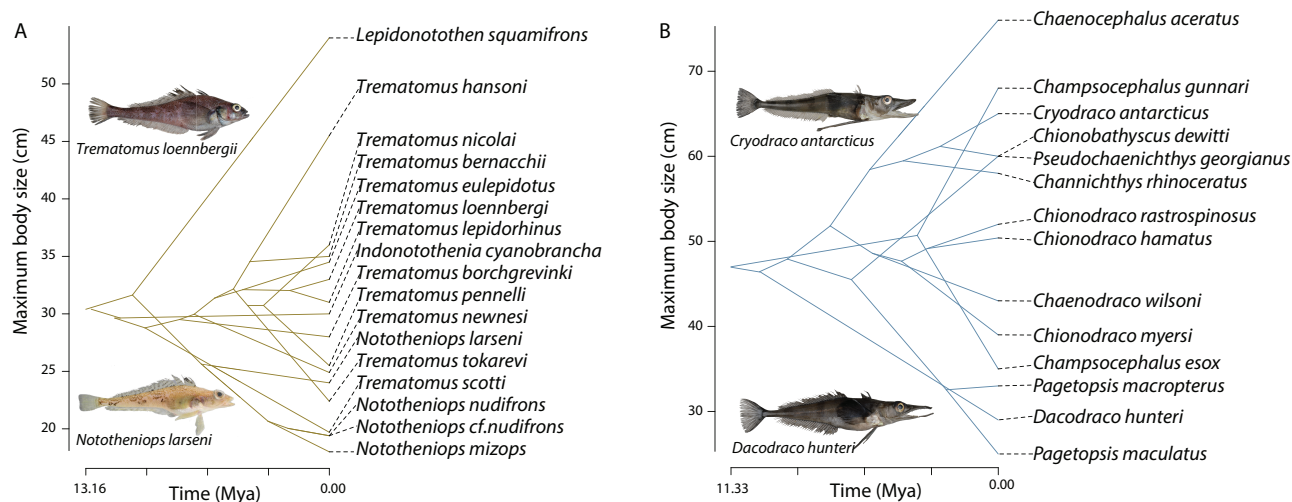


Figure 5: Evolutionary history of maximum body size demonstrates several instances of convergence of distantly related species in aspects of body shape as well as striking divergences among closely related species. *A* represents projection of notoperch phylogeny, and *B* represents projection of crocodile icefish phylogeny. In both panels, the *x*-axis corresponds to time in millions of years, with branch lengths of phylogeny reflecting estimated divergence times. The *y*-axis represents variation in maximum body size, with tip placement along the *y*-axis reflecting maximum body size reported for that species. Carl D. Struthers (National Museum of New Zealand) and Peter Marriott (National Institute of Water and Atmospheric Research of New Zealand) provided photographs of *Cryodraco antarcticus*, *Dacodraco hunteri*, *Nototheniops larseni*, and *Trematomus loennbergii*.

Evidence for Correlated Evolution among Traits

Diversification along the benthic–pelagic axis of the water column is commonly associated with parallel divergences in fish body shape, where shifts from benthic to pelagic habitats are often accompanied by evolutionary transitions from deep-bodied forms to more slender fusiform body shapes (Rundle et al. 2000; Hulsey et al. 2013; Tavera et al. 2018). However, we find no evidence that repeated diversification along the benthic–pelagic axis of the water column has significantly influenced changes in body depth in either of our focal radiations (tables S5–S10). These counterintuitive findings about icefish and notoperch ecomorphological diversification are likely explained by the fact that many cryonotothenioid species are known to periodically forage outside of their position along the buoyancy-based biotope axis (Casaux and Barrera-Oro 2013; Eastman 2020). This potential ecological plasticity could consequently reduce the expected tight correlations between body shape and niche use in icefishes and notoperches (table S5). Future work investigating the relationship between other axes of phenotypic diversification, such as fin shape or body width, and patterns of diversification in prey and habitat utilization in these radiations are warranted.

Body size represents another important axis of phenotypic diversification in many evolutionary radiations, with a hypothesized positive relationship between body size and mean depth occupancy (Merrett and Haedrich 1997). However, similar to patterns observed for body shape, we find no correlations between notothenioid body size variation and

disparity in either diet or depth (tables S7–S10). Instead, two species of icefish that lie at either extreme of variation in body size, *Dacodraco hunteri* and *Channichthys rhinoceros* (fig. 5B), occupy a nearly identical point in diet space, reflecting convergence on piscivory (fig. 1A). Similarly, one of the smallest notoperch species (*Trematomus scotti*) and one of the largest notoperch species (*Trematomus hansonii*) each rely primarily on polychaetes as a prey resource (fig. S2). One explanation for this lack of correlation is that many cryonotothenioid species appear to be opportunistic feeders, often pursuing the prey resources that are most abundant in a given season or locality (Hopkins 1987; La Mesa et al. 2004; Casaux and Barrera-Oro 2013). Moreover, the lack of correlation between body size and depth, diet, or buoyancy provides no evidence to suggest that patterns of habitat and resource utilization are constrained by body size. Taken together, our results suggest that the ecological plasticity that characterizes many cryonotothenioid species spanning a range of body sizes and shapes has likely been integral to the persistence and diversification of this clade as availability of prey resources and different depth habitats fluctuated during repeated glacial disturbances of the Antarctic continental shelf.

Repeated Ecomorphological Diversification in Icefishes and Notoperches

Trait disparity among closely related species is expected to decline as a result of niche filling (Simpson 1953; Schluter

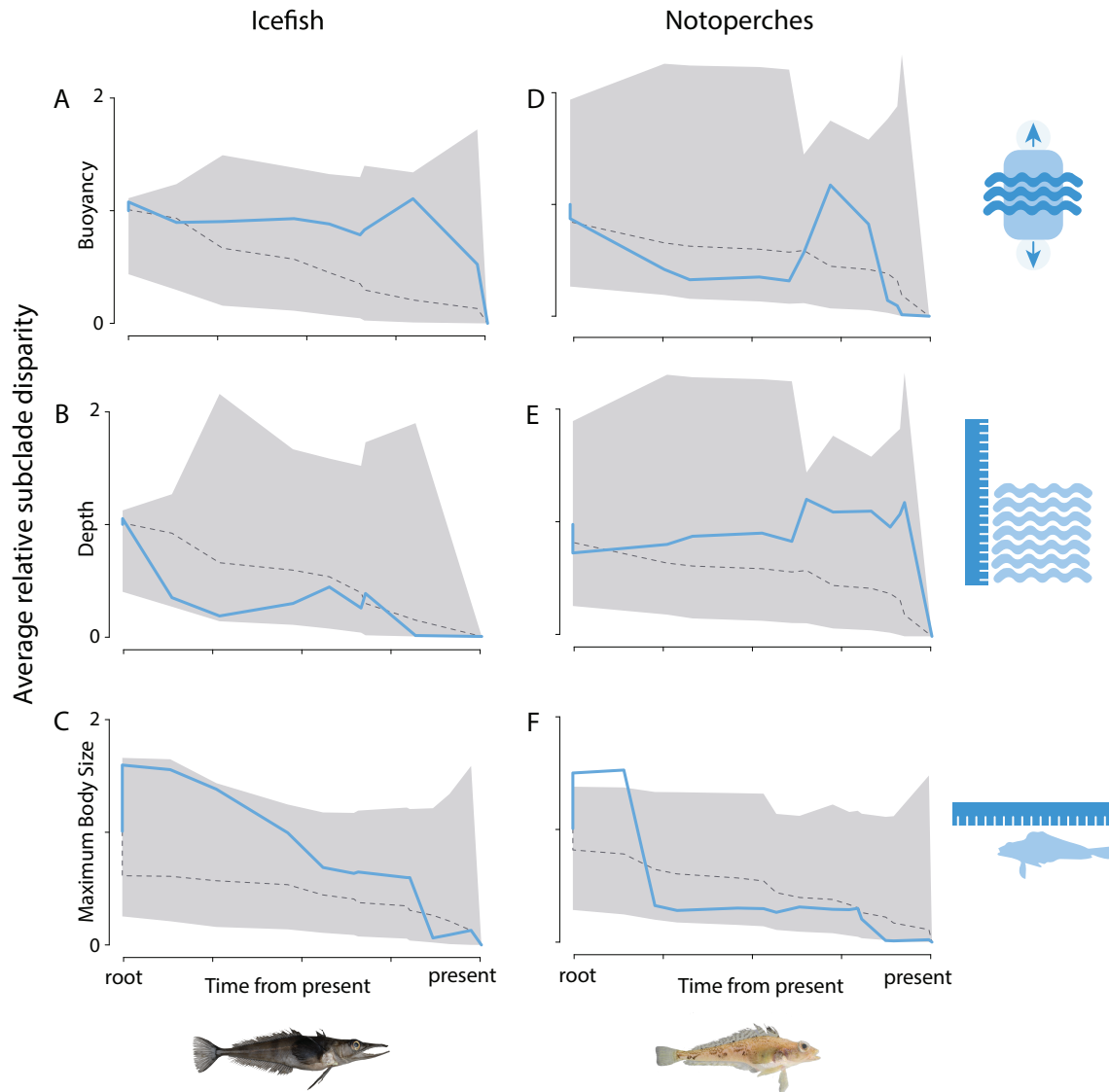


Figure 6: Disparity-through-time (DTT) analyses generally reveal patterns of high average subclade trait disparity within both focal radiations. Panels contrast icefish buoyancy (A), mean depth (B), and maximum body size (C) DTT to patterns exhibited in notoperch buoyancy (D), mean depth (E), and maximum body size (F). Solid lines depict empirical estimation of DTT, and dashed lines represent the mean DTT across 10,000 Brownian motion simulations. Shaded regions depict the 95% confidence interval of the Brownian motion simulation. The x-axis is proportional to the time between the present and the timing of each clade's most recent common ancestor (root node). Carl D. Struthers (National Museum of New Zealand) and Peter Marriott (National Institute of Water and Atmospheric Research of New Zealand) provided photographs of *Dacodraco hunteri* and *Nototheniops larseni*.

2000) and/or a loss of genetic variability through time as lineages become increasingly specialized (West-Eberhard 2003; Gibert 2017). However, within each of the icefish and notoperch radiations, we find that trait disparity is often higher within subclades than between subclades (fig. 6), a pattern that suggests repeated diversification of species into overlapping regions of trait space. Moreover, our visualizations of water column usage (figs. 2, 3), body shape (fig. 4) and size (fig. 5), and diet (fig. 1) each demonstrate

numerous cases of trait convergence among distantly related species and high divergences among close relatives. Most strikingly, we frequently observe the highest levels of trait divergence between sister species. For instance, the sister species *Trematomus lepidorhinus* and *Trematomus loennbergii* occupy opposite extremes of variation along the first PC axis of prey usage, with *T. lepidorhinus* feeding mostly on amphipods and polychaetes, while *T. loennbergii* mostly utilizes copepods (figs. 1D, S2). Within

icefishes, sister species *Champscephalus esox* and *Champscephalus gunnari* similarly sit at opposite ends of the third PC axis of diet variation, with *C. esox* consuming mostly fish while *C. gunnari* feeds primarily on krill (figs. 1C, S1). These findings of high trait divergence among closely related species suggest that ecological and phenotypic diversification have occurred at recent timescales within both icefishes and notoperches.

Whether or not a lineage radiates in response to emergent ecological opportunities depends in large part on the ability of that lineage to readily adapt to the available niches (Stroud and Losos 2016). Across all of the studied traits, divergences among closely related species are occurring at very short timescales, suggesting a high level of trait lability in cryonotothenioids. For the key ecological trait of buoyancy, high trait lability is almost certainly the case. Recent work using CRISPR-Cas9 has experimentally validated that the modulation of a suite of genes associated with human degenerative bone diseases dramatically alters skeletal ossification and yields a range of skeletal phenotypes in notothenioids (Daane et al. 2019). This genetic mechanism may explain the complex multimodal depth distributions we observe for several species, suggesting a range of potential phenotypes for selection to act on during times of environmental change that allow lineages to take advantage of emergent ecological opportunities. Genomic evidence from island lineages has revealed suites of genes responsible for rapid evolution of body size and skeletal shape (Gray et al. 2015; Parmenter et al. 2016). It is possible that divergence along similar genetic pathways has enabled notothenioids to alter their buoyancy to take advantage of resources in newly assembling communities. Our results highlight that future genomic work focused on the evolution of the notothenioid bauplan, such as genome-wide association studies or notothenioid-guided genome editing in model organisms, is an incredibly promising and exciting research frontier.

Impacts of Range Overlap and Clade Age on Trait Divergence

Coexistence of closely related species in adaptive radiations is frequently attributed to character displacement (Tobias et al. 2014; Gillespie et al. 2020), which is expected to promote increased trait divergences among species pairs that occur in sympatry (Dayan and Simberloff 2005; Pfennig and Pfennig 2009). Alternatively, trait divergence could be better predicted by time since common ancestry than by range overlap, where higher trait divergences may be expected given a greater amount of evolutionary time afforded for accumulation of trait differences. However, we find limited evidence to suggest that either range overlap or clade age significantly predicts patterns of trait divergences

within either crocodile icefishes or notoperches (tables S11, S12). We propose that the lack of strong evidence for increased trait divergence among sympatric species pairs is likely driven by repeated convergent evolution among distantly related species along axes of habitat and feeding niche use. Although this finding of rampant convergence in sympatry seems paradoxical, it could be explained by a pattern of niche complementarity. Species that have converged along one dimension of niche space may be sufficiently divergent along another niche dimension that the competitive interactions among them are minimized, thereby facilitating their coexistence in a given area (Schoener 1974; Werner 1977; Losos et al. 2003). For example, the sympatric icefish species *Chionobathyscus dewitti* and *D. hunteri* converge in buoyancy yet diverge in prey usage. *Chionobathyscus dewitti* consumes primarily cephalopods, while the diet of *D. hunteri* consists primarily of fish (figs. 1A–1C, S1). Additionally, the sympatrically distributed notoperch species *Trematomus eulepidotus* and *Trematomus newnesi* exhibit considerable convergence in prey usage (fig. 1D–1F) yet appear to partition the water column: *T. newnesi* occurs primarily in shallow-water habitats (mean depth = 160 m), while *T. eulepidotus* typically occupies deeper-water habitats (mean depth = 389 m; fig. 3; table S1). These and other potential cases of niche complementarity suggest a potential role of interspecific interactions in generating ecomorphological disparity and may explain why convergences among species along the benthic-pelagic axis of the water column are not associated with parallel convergences in bathymetric distribution or prey use (tables S5–S10). Given the general lack of correlation between body shape and buoyancy, diet, or depth, future studies investigating how cryonotothenioids utilize distinct strategies to occupy the same feeding niche and achieve high niche lability will be critical to characterizing the mechanisms of diversification that have shaped this unusual adaptive radiation.

Conclusions

The results of this study reflect a dynamic history of near-shore Antarctic marine habitats, in which benthic communities are subjected to repeated catastrophic events at large geographic scales that decimate their fauna (Huybrechts 2002; Thatje et al. 2005, 2008; Near et al. 2012; Dornburg et al. 2017). The wake of these events has likely facilitated the repeated generation of ecological opportunities for diversification and may be considered analogous to an experiment in which the early stages of adaptive radiation are iteratively repeated (Near et al. 2012). In many ways, this background of widespread environmental devastation and recovery is not unique to the Antarctic. On the contrary, pulses of environmental change have occurred throughout the Cenozoic, not only promoting local extirpation or the

extinction of species at large spatial scales but also generating novel ecological opportunities that are correlated with the evolution of phenotypic disparity (Lucek et al. 2018; Folk et al. 2019). As such, our finding that periodic environmental disturbance has promoted the rapid ecomorphological divergence among close relatives that, in turn, results in high levels of convergence among distant relatives may represent a general feature of evolutionary diversification in highly dynamic environments.

Acknowledgments

Fieldwork was facilitated through the US Antarctic Marine Living Resources Program and the officers and crew of the research vessel *Yuzhmorgeologia* and the 2004 ICEFISH cruise aboard the research vessel/icebreaker Nathaniel B. Palmer. G. Watkins-Colwell, and O. Orr provided support with museum collections. Field and laboratory support were provided by H. W. Detrich, J. Kendrick, K.-H. Kock, J. A. Moore, A. L. Stewart, and P. J. McMillan. C. D. Struthers (National Museum of New Zealand) and P. Marriott (National Institute of Water and Atmospheric Research of New Zealand) provided photographs of *Cryodraco antarcticus*, *Dacodraco hunteri*, *Nototheniops larseni*, and *Trematomus loennbergii* used in figures 5 and 6. We thank Editor D. I. Bolnick, Associate Editor D. L. Rabosky, and two anonymous reviewers for thoughtful comments and suggestions that significantly improved the manuscript. We are grateful to all who provided helpful discussion and feedback on earlier versions of the manuscript, including C. W. Dunn, E. J. Edwards, and colleagues and members of the Near, Dornburg, Donoghue, and Muñoz labs. This work was supported in part by the Refugia and Ecosystem Tolerance in the Southern Ocean project (RECTO; BR/154/A1/RECTO) funded by the Belgian Science Policy Office.

Statement of Authorship

T.J.N. and A.D. conceptualized this study. E.P., K.L.Z., C.D.J., T.J.N., and A.D. contributed to data collection. E.P., K.L.Z., J.Y., B.F., and A.D. contributed to data analysis and data visualization. E.P. and A.D. wrote the original draft of the manuscript. All authors contributed to writing and revising the final draft of the manuscript.

Data and Code Availability

All data generated in this study are available from the Dryad Digital Repository (<https://doi.org/10.5061/dryad.bk3j9kdbg>; Parker et al. 2022). Sequence data collected from previous studies are available from Zenodo (<https://doi.org/10.5281/zenodo.1406314>). All code generated in this study is available from Zenodo (<https://doi.org/10.5281/zenodo.6464044>).

Literature Cited

- Adams, D., M. Collyer, A. Kaliontzopoulou, and E. Baken. 2021. geomorph: software for geometric morphometric analyses. R package version 4.0.2. <https://cran.r-project.org/package=geomorph>.
- Allcock, A. L., and J. M. Strugnell. 2012. Southern Ocean diversity: new paradigms from molecular ecology. *Trends in Ecology and Evolution* 27:520–528.
- Arbour, J. H., and H. López-Fernández. 2013. Ecological variation in South American geophagine cichlids arose during an early burst of adaptive morphological and functional evolution. *Proceedings of the Royal Society B* 280:20130849.
- Baken, E. K., M. L. Collyer, A. Kaliontzopoulou, and D. C. Adams. 2021. geomorph v4.0 and gmShiny: enhanced analytics and a new graphical interface for a comprehensive morphometric experience. *Methods in Ecology and Evolution* 12:2355–2363.
- Benjamini, Y., and Y. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society B* 57:289–300.
- Borko, Š., P. Trontelj, O. Seehausen, A. Moškrič, and C. Fišer. 2021. A subterranean adaptive radiation of amphipods in Europe. *Nature Communications* 12:1–12.
- Casaux, R., and E. Barrera-Oro. 2013. Dietary overlap in inshore notothenioid fish from the Danco Coast, western Antarctic Peninsula. *Polar Research* 32:21319.
- Colombo, M., M. Damerou, R. Hanel, W. Salzburger, and M. Matschiner. 2015. Diversity and disparity through time in the adaptive radiation of Antarctic notothenioid fishes. *Journal of Evolutionary Biology* 28:376–394.
- Daane, J. M., A. Dornburg, P. Smits, D. J. MacGuigan, M. B. Hawkins, T. J. Near, H. W. Detrich III, and M. P. Harris. 2019. Historical contingency shapes adaptive radiation in Antarctic fishes. *Nature Ecology and Evolution* 3:1102–1109.
- Dayan, T., and D. Simberloff. 2005. Ecological and community-wide character displacement: the next generation. *Ecology Letters* 8:875–94.
- Dornburg, A., S. Federman, R. I. Eytan, and T. J. Near. 2016. Cryptic species diversity in sub-Antarctic islands: a case study of Lepidotothen. *Molecular Phylogenetics and Evolution* 104:32–43.
- Dornburg, A., S. Federman, A. D. Lamb, C. D. Jones, and T. J. Near. 2017. Cradles and museums of Antarctic teleost biodiversity. *Nature Ecology and Evolution* 9:1379–1384.
- Drummond, A. J., and R. R. Bouckaert. 2015. Bayesian evolutionary analysis with BEAST. Cambridge University Press, Cambridge.
- Drummond, A. J., M. A. Suchard, D. Xie, and A. Rambaut. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution* 29:1969–1973.
- Eastman, J. T. 1993. Antarctic fish biology: evolution in a unique environment. Academic Press, San Diego.
- . 2005. The nature of the diversity of Antarctic fishes. *Polar Biology* 28:93–107.
- . 2017. Bathymetric distributions of notothenioid fishes. *Polar Biology* 40:2077–2095.
- . 2019. An analysis of maximum body size and designation of size categories for notothenioid fishes. *Polar Biology* 42:1131–1145.
- . 2020. The buoyancy-based biotope axis of the evolutionary radiation of Antarctic cryonotothenioid fishes. *Polar Biology* 43:1217–1231.
- Fitzpatrick, L., C. F. Parmeter, and J. Agar. 2019. Approaches for visualizing uncertainty in benefit transfer from meta-regression. *Ecological Economics* 164:106344.

- Folk, R. A., R. L. Stubbs, M. E. Mort, N. Cellinese, J. M. Allen, P. S. Soltis, D. E. Soltis, and R. P. Guralnick. 2019. Rates of niche and phenotype evolution lag behind diversification in a temperate radiation. *Proceedings of the National Academy of Sciences of the USA* 116:10874–10882.
- García-Navas, V., M. Rodríguez-Rey, and M. Westerman. 2018. Bursts of morphological and lineage diversification in modern dasyurids, a “classic” adaptive radiation. *Biological Journal of the Linnean Society* 123:782–795.
- Gibert, J.-M. 2017. The flexible stem hypothesis: evidence from genetic data. *Development Genes and Evolution* 227:297–307.
- Gillespie, R. G., G. M. Bennett, L. De Meester, J. L. Feder, R. C. Fleischer, L. J. Harmon, A. P. Hendry, et al. 2020. Comparing adaptive radiations across space, time, and taxa. *Journal of Heredity* 111:1–20.
- Grant, P. R. 1986. *Ecology and evolution of Darwin’s finches*. Princeton University Press, Princeton.
- Gray, M. M., M. D. Parmenter, C. A. Hogan, I. Ford, R. J. Cuthbert, P. G. Ryan, K. W. Broman, and B. A. Payseur. 2015. Genetics of rapid and extreme size evolution in island mice. *Genetics* 201:213–228.
- Hadfield, J. D. 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software* 33:1–22.
- Harmon, L. J., J. A. Schulte II, A. Larson, and J. B. Losos. 2003. Tempo and mode of evolutionary radiation in iguanian lizards. *Science* 301:961–964.
- Hopkins, T. L. 1987. Midwater food web in McMurdo Sound, Ross Sea, Antarctica. *Marine Biology* 96:93–106.
- Hulsey, C. D., R. J. Roberts, Y.-H. E. Loh, M. F. Rupp, and J. T. Streebman. 2013. Lake Malawi cichlid evolution along a benthic/limnetic axis. *Ecology and Evolution* 3:2262–2272.
- Huybrechts, P. 2002. Sea-level changes at the LGM from ice-dynamic reconstructions of the Greenland and Antarctic ice sheets during the glacial cycles. *Quaternary Science Reviews* 21:203–231.
- Ivory, S. J., M. W. Blome, J. W. King, M. M. McGlue, J. E. Cole, and A. S. Cohen. 2016. Environmental change explains cichlid adaptive radiation at Lake Malawi over the past 1.2 million years. *Proceedings of the National Academy of Sciences of the USA* 113:11895–11900.
- La Mesa, M., J. T. Eastman, and M. Vacchi. 2004. The role of notothenioid fish in the food web of the Ross Sea shelf waters: a review. *Polar Biology* 27:321–338.
- Losos, J. 2009. *Lizards in an evolutionary tree*. University of California Press, Berkeley.
- Losos, J. B., M. Leal, R. E. Glor, K. De Queiroz, P. E. Hertz, L. Rodríguez Schettino, A. C. Lara, T. R. Jackman, and A. Larson. 2003. Niche lability in the evolution of a Caribbean lizard community. *Nature* 424:542–545.
- Lucek, K., I. Keller, A. W. Nolte, and O. Seehausen. 2018. Distinct colonization waves underlie the diversification of the freshwater sculpin (*Cottus gobio*) in the Central European Alpine region. *Journal of Evolutionary Biology* 31:1254–1267.
- Matschiner, M., R. Hanel, and W. Salzburger. 2011. On the origin and trigger of the notothenioid adaptive radiation. *PLoS ONE* 6: e18911.
- Merrett, N. R., and R. L. Haedrich. 1997. Deep-sea demersal fish and fisheries. *Fish and Fisheries Series*. Vol. 23. Springer, Dordrecht.
- Near, T. J., A. Dornburg, K. L. Kuhn, J. T. Eastman, J. N. Pennington, T. Patarnello, L. Zane, D. A. Fernández, and C. D. Jones. 2012. Ancient climate change, antifreeze, and the evolutionary diversification of Antarctic fishes. *Proceedings of the National Academy of Sciences of the USA* 109:3434–3439.
- Near, T. J., D. J. MacGuigan, E. Parker, C. D. Struthers, C. D. Jones, and A. Dornburg. 2018. Phylogenetic analysis of Antarctic notothenioids illuminates the utility of RADseq for resolving Cenozoic adaptive radiations. *Molecular Phylogenetics and Evolution* 129:268–279.
- O’Loughlin, P. M., G. Paulay, N. Davey, and F. Michonneau. 2011. The Antarctic region as a marine biodiversity hotspot for echinoderms: diversity and diversification of sea cucumbers. *Deep Sea Research II* 58:264–275.
- Osborn, H. F. 1902. The law of adaptive radiation. *American Naturalist* 36:353–363.
- Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20:289–290.
- Parker, E., K. L. Zapfe, J. Yadav, B. Frédéric, C. D. Jones, E. P. Economo, S. Federman, T. J. Near, and A. Dornburg. 2022. Data from: Periodic environmental disturbance drives repeated ecomorphological diversification in an adaptive radiation of Antarctic fishes. *American Naturalist*, Dryad Digital Repository, <https://doi.org/10.5061/dryad.bk3j9kdbg>.
- Parmenter, M. D., M. M. Gray, C. A. Hogan, I. N. Ford, K. W. Broman, C. J. Vinyard, and B. A. Payseur. 2016. Genetics of skeletal evolution in unusually large mice from Gough Island. *Genetics* 204:1559–1572.
- Pennell, M. W., J. M. Eastman, G. J. Slater, J. W. Brown, J. C. Uyeda, R. G. FitzJohn, M. E. Alfaro, and L. J. Harmon. 2014. geiger v2.0: an expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. *Bioinformatics* 30:2216–2218.
- Pfennig, K. S., and D. W. Pfennig. 2009. Character displacement: ecological and reproductive responses to a common evolutionary problem. *Quarterly Review of Biology* 84:253–276.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, S. Heisterkamp, B. Van Willigen, and R. Maintainer. 2017. nlme: linear and nonlinear mixed effects models. R package version 3:109. <https://CRAN.R-project.org/package=nlme>.
- Pouchon, C., A. Fernández, J. M. Nassar, F. Boyer, S. Aubert, S. Lavergne, and J. Mavárez. 2018. Phylogenomic analysis of the explosive adaptive radiation of the *Espeletia* complex (Asteraceae) in the tropical Andes. *Systematic Biology* 67:1041–1060.
- Price, S. L., R. S. Etienne, and S. Powell. 2016. Tightly congruent bursts of lineage and phenotypic diversification identified in a continental ant radiation. *Evolution* 70:903–912.
- Rabosky, D. L., J. Chang, P. O. Title, P. F. Cowman, L. Sallan, M. Friedman, K. Kaschner, et al. 2018. An inverse latitudinal gradient in speciation rate for marine fishes. *Nature* 559:392–395.
- Revell, L. J. 2011. phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecology and Evolution* 3:217–223.
- Rohlf, F. J., and D. Slice. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Biology* 39:40–59.
- Rundle, H. D., L. Nagel, J. W. Boughman, and D. Schluter. 2000. Natural selection and parallel speciation in sympatric sticklebacks. *Science* 287:306–308.
- Rutschmann, S., M. Matschiner, M. Damerau, M. Muschick, M. F. Lehmann, R. Hanel, and W. Salzburger. 2011. Parallel ecological diversification in Antarctic notothenioid fishes as evidence for adaptive radiation. *Molecular Ecology* 20:4707–4721.

- Schluter, D. 2000. The ecology of adaptive radiation. Oxford University Press, Oxford.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. *Science* 185:27–39.
- Simpson, G. G. 1944. Tempo and mode in evolution. Columbia University Press, New York.
- . 1953. The major features of evolution. Columbia University Press, New York.
- Slater, G. J., S. A. Price, F. Santini, and M. E. Alfaro. 2010. Diversity versus disparity and the radiation of modern cetaceans. *Proceedings of the Royal Society B* 277:3097–3104.
- Smale, D. A., K. M. Brown, D. K. A. Barnes, K. P. P. Fraser, and A. Clarke. 2008. Ice scour disturbance in Antarctic waters. *Science* 321:371.
- Stroud, J. T., and J. B. Losos. 2016. Ecological opportunity and adaptive radiation. *Annual Review of Ecology, Evolution, and Systematics* 47:507–532.
- Tavera, J., A. Acero P., and P. C. Wainwright. 2018. Multilocus phylogeny, divergence times, and a major role for the benthic-to-pelagic axis in the diversification of grunts (Haemulidae). *Molecular Phylogenetics and Evolution* 121:212–223.
- Thatje, S., C.-D. Hillenbrand, and R. Larter. 2005. On the origin of Antarctic marine benthic community structure. *Trends in Ecology and Evolution* 20:534–540.
- Thatje, S., C.-D. Hillenbrand, A. Mackensen, and R. Larter. 2008. Life hung by a thread: endurance of Antarctic fauna in glacial periods. *Ecology* 89:682–692.
- Tobias, J. A., C. K. Cornwallis, E. P. Derryberry, S. Claramunt, R. T. Brumfield, and N. Seddon. 2014. Species coexistence and the dynamics of phenotypic evolution in adaptive radiation. *Nature* 506:359–363.
- Tripathi, A. K., C. D. Roberts, and R. A. Eagle. 2009. Coupling of CO₂ and ice sheet stability over major climate transitions of the last 20 million years. *Science* 326:1394–1397.
- Uyeda, J. C., D. S. Caetano, and M. W. Pennell. 2015. Comparative analysis of principal components can be misleading. *Systematic Biology* 64:677–689.
- Werner, E. E. 1977. Species packing and niche complementarity in three sunfishes. *American Naturalist* 111:553–578.
- West-Eberhard, M. J. 2003. Developmental plasticity and evolution. Oxford University Press, New York.
- Wilson, N. G., J. A. Maschek, and B. J. Baker. 2013. A species flock driven by predation? secondary metabolites support diversification of slugs in Antarctica. *PLoS ONE* 8:e80277.
- Zelditch, M. L., D. L. Swiderski, and H. D. Sheets. 2012. Geometric morphometrics for biologists: a primer. Academic Press, Amsterdam.
- Brenner, M., B. H. Buck, S. Cordes, L. Dietrich, U. Jacob, K. Mintenbeck, A. Schroeder, T. Brey, R. Knust, and W. Arntz. 2001. The role of iceberg scours in niche separation within the Antarctic fish genus *Trematomus*. *Polar Biology* 24:502–507.
- Bushula, T., E. Pakhomov, S. Kaehler, S. Davis, and R. Kalin. 2005. Diet and daily ration of two nototheniid fish on the shelf of the sub-Antarctic Prince Edward Islands. *Polar Biology* 28:585–593.
- Casaux, R., E. Barrera-Oro, A. Baroni, and A. Ramón. 2003. Ecology of inshore nototheniid fish from the Danco Coast, Antarctic Peninsula. *Polar Biology* 26:157–165.
- Casaux, R. J., A. S. Mazzotta, and E. Barrera-Oro. 1990. Seasonal aspects of the biology and diet of nearshore nototheniid fish at Potter Cover, South Shetland Islands, Antarctica. *Polar Biology* 11:63–72.
- Curcio, N., A. Tombari, and F. Capitano. Otolith morphology and feeding ecology of an Antarctic nototheniid, *Lepidonotothen larseni*. *Antarctic Science* 26:124–132.
- Daniels, R. A. 1982. Feeding ecology of some fishes of the Antarctic Peninsula. *Fishery Bulletin* 80:575–588.
- DeWitt, H. H., P. C. Heemstra, and O. Gon. 1990. Nototheniidae. Pages 279–331 in O. Gon and P. C. Heemstra, eds. *Fishes of the Southern Ocean*. JLB Smith Institute of Ichthyology, Grahamstown, South Africa.
- Dornburg, A., B. Sidlauskas, F. Santini, L. Sorenson, T. J. Near, and M. E. Alfaro. 2011. The influence of an innovative locomotor strategy on the phenotypic diversification of triggerfish (family: Balistidae). *Evolution* 65:1912–1926.
- Eastman, J. T. 1985. *Pleuragramma antarcticum* (Pisces, Nototheniidae) as food items for other fishes in McMurdo Sound, Antarctica. *Polar Biology* 4:155–160.
- . 1999. Aspects of the biology of the icefish *Dacodraco hunteri* (Notothenioidei, Channichthyidae) in the Ross Sea, Antarctica. *Polar Biology* 21:194–196.
- Eastman, J. T., and A. L. DeVries. 1982. Buoyancy studies of nototheniid fishes in McMurdo Sound, Antarctica. *Copeia* 1982:385–393.
- Flores, H., K.-H. Kock, S. Wilhelms, and C. D. Jones. 2004. Diet of two icefish species from the South Shetland Islands and Elephant Island, *Champscephalus gunnari* and *Chaenocephalus aceratus*. *Polar Biology* 27:119–129.
- Foster, B. A., and J. C. Montgomery. 1993. Planktivory in benthic nototheniid fish in McMurdo Sound, Antarctica. *Environmental Biology of Fishes* 36:313–318.
- Frédérich, B., O. Colleye, G. Lepoint, and D. Lecchini. 2012. Mismatch between shape changes and ecological shifts during the post-settlement growth of the surgeonfish, *Acanthurus triostegus*. *Frontiers in Zoology* 9:8.
- Frédérich, B., G. Maramà, G. Carnevale, and F. Santini. 2016. Non-reef environments impact the diversification of extant jacks, remoras and allies (Carangoidei, Percomorpha). *Proceedings of the Royal Society B* 283:20161556.
- Gon, O., and P. C. Heemstra. 1990. *Fishes of the Southern Ocean*. JLB Smith Institute of Ichthyology, Grahamstown, South Africa.
- Gröhsler, T. 1992. Nahrungsökologische Untersuchungen an antarktischen Fischen um Elephant Island unter besonderer Berücksichtigung des Südwinters. *Mitteilungen aus dem Institut für Sefischerei* 47:1–296.
- Hubold, G. 1984. Spatial distribution of *Pleuragramma antarcticum* (Pisces: Nototheniidae) near the Filchner and Larsen ice shelves (Weddell sea/Antarctica). *Polar Biology* 3:231–236.
- Hureau, J. C. 1966. Biologie de *Chaenichthys rhinoceratus* Richardson, et probleme du sang incolore des Chaenichthyidae, poissons

References Cited Only in the Online Enhancements

- Aguilar-Medrano, R., B. Frédéric, and P. H. Barber. 2016. Modular diversification of the locomotor system in damselfishes (Pomacentridae). *Journal of Morphology* 277:603–614.
- Barrera-Oro, E. 2003. Analysis of dietary overlap in Antarctic fish (Notothenioidei) from the South Shetland Islands: no evidence of food competition. *Polar Biology* 26:631–637.
- Barrera-Oro, E., R. Casaux, and E. Marschoff. 1998. Analysis of the diet of *Champscephalus gunnari* at South Georgia in late summer from 1994 to 1997, Dr Eduardo L. Holmberg surveys. *CCAML Science* 5:103–123.

- des mers australes. Bulletin de la Societe Zoologique de France 91:735–751.
- Iwami, T., and K.-H. Kock. 1990. Channichthyidae. Pages 381–399 in O. Gon and P. C. Heemstra, eds. Fishes of the Southern Ocean. JLB Smith Institute of Ichthyology, Grahamstown, South Africa.
- Kiest, K. A. 1993. A relationship of diet to prey abundance and the foraging behavior of *Trematomus bernacchii*. Polar Biology 13:291–296.
- Kock, K.-H. 2005. Antarctic icefishes (Channichthyidae): a unique family of fishes: a review. I. Polar Biology 28:862–895.
- Kock, K.-H., and C. D. Jones. 2002. The biology of the icefish *Cryodraco antarcticus* Dollo, 1900 (Pisces, Channichthyidae) in the southern Scotia Arc (Antarctica). Polar Biology 25:416–424.
- Kock, K.-H., C. D. Jones, and S. Wilhelms. 2000. Biological characteristics of Antarctic fish stocks in the southern Scotia Arc region. CCAMLR Science 7:1–41.
- Kock, K.-H., L. Pshenichnov, C. D. Jones, J. Grorger, and R. Riehl. 2008. The biology of the spiny icefish *Chaenodraco wilsoni* Regan, 1914. Polar Biology 31:381–393.
- Kock, K.-H., S. Wilhelms, I. Everson, and J. Groeger. 1994. Variations in the diet composition and feeding intensity of mackerel icefish *Champocephalus gunnari* at South Georgia (Antarctic). Marine Ecology Progress Series 108:43–57.
- La Mesa, M., M. Dalu, and M. Vacchi. 2004. Trophic ecology of the emerald notothen, *Trematomus bernacchii* (Pisces, Nototheniidae) from Terra Nova Bay, Ross Sea, Antarctica. Polar Biology 27:721–728.
- La Mesa, M., M. Vacchi, A. Castelli, and G. Diviacco. 1997. Feeding ecology of two nototheniid fishes, *Trematomus hansonii* and *Trematomus loennbergii*, from Terra Nova Bay, Ross Sea. Polar Biology 17:62–68.
- La Mesa, M., M. Vacchi, and T. Z. Sertorio. 2000. Feeding plasticity of *Trematomus newnesi* (Pisces, Nototheniidae) in Terra Nova Bay, Ross Sea, in relation to environmental conditions. Polar Biology 23:38–45.
- Linkowski, T., P. Presler, and C. Zukowski. 1983. Food habits of nototheniid fishes (Nototheniidae) in Admiralty Bay (King George Island, South Shetland Islands). Polish Polar Research 4:79–96.
- Main, C. E., M. A. Collins, R. Mitchell, and M. Belchier. 2009. Identifying patterns in the diet of mackerel icefish (*Champocephalus gunnari*) at South Georgia using bootstrapped confidence intervals of a dietary index. Polar Biology 32:569–581.
- McKenna, J. E. 1991. Trophic relationships within the Antarctic demersal fish community of South Georgia Island. Fishery Bulletin 89:643–654.
- Mintenbeck, K. 2009. Trophic interactions within high Antarctic shelf communities: food web structure and significance of fish. PhD diss. University of Bremen, Germany.
- Montgomery, J. C., B. A. Foster, R. C. Milton, and E. Carr. 1993. Spatial and temporal variations in the diet of nototheniid fish in McMurdo Sound, Antarctica. Polar Biology 13:429–431.
- Moreno, C. A. 1980. Observations of food and reproduction in *Trematomus bernacchii* (Pisces: Nototheniidae) from the Palmer Archipelago, Antarctica. Copeia 1980:171–173.
- Moreno, C. A., and F. Jara. 1984. Ecological studies on fish fauna associated with *Macrocystis pyrifera* belts in the south of Fuegoian Islands, Chile. Marine Ecology Progress Series Oldendorf 15:99–107.
- Near, T. J., S. E. Russo, C. D. Jones, and A. L. DeVries. 2003. Ontogenetic shift in buoyancy and habitat in the Antarctic toothfish, *Dissostichus mawsoni* (Perciformes: Nototheniidae). Polar Biology 26:124–128.
- Petrov, A. 2011. New data on the diet of deep-sea icefish *Chionobathyscus dewitti* (Channichthyidae) in the Ross Sea in 2010. Journal of Ichthyology 51:692–694.
- Rambaut, A. 2013. Analysis of variable sites only in BEAST or MrBayes. BEAST Users Forum, September 19, 2013, https://groups.google.com/g/beast-users/c/V5vRghILMfw/m/jMtC_DwS5EYJ.
- Reid, W. D., S. Clarke, M. A. Collins, and M. Belchier. 2007. Distribution and ecology of *Chaenocephalus aceratus* (Channichthyidae) around South Georgia and Shag Rocks (Southern Ocean). Polar Biology 30:1523–1533.
- Rohlf, F. J. 2010. TpsDig2. State University of New York, Stony Brook.
- Sutton, C., M. Manning, D. Stevens, and P. Marriott. 2008. Biological parameters for icefish (*Chionobathyscus dewitti*) in the Ross Sea, Antarctica. CCAMLR Science 15:139–165.
- Takahashi, M. 1983. Trophic ecology of demersal fish community north of the South Shetland Islands, with notes on the ecological role of krill. Memoirs of the National Institute of Polar Research 27:183–192.
- Takahashi, M., and T. Iwami. 1997. The summer diet of demersal fish at the South Shetland Islands. Antarctic Science 9:407–413.
- Takahashi, M., and T. Nemoto. 1984. The food of some Antarctic fish in the western Ross Sea in the summer of 1979. Polar Biology 3:237–240.
- Terauds, A., S. L. Chown, F. Morgan, H. J. Peat, D. J. Watts, H. Keys, P. Convey, and D. M. Bergstrom. 2012. Conservation biogeography of the Antarctic. Diversity and Distributions 18:726–741.
- Tyler, P., and T. Paul. 2016. Biogeographic atlas of the Southern Ocean. Pages 328–362 in C. de Broyer and P. Koubbi, eds. Scientific Committee on Antarctic Research, Cambridge.
- Vacchi, M., and M. La Mesa. 1995. Diet of the Antarctic fish *Trematomus newnesi* Boulenger, 1902 (Nototheniidae) from Terra Nova Bay, Ross Sea. Antarctic Science 7:37–38.
- Vacchi, M., M. La Mesa, and M. Greco. 2000. The coastal fish fauna of Terra Nova Bay, Ross Sea, Antarctica. Pages 457–468 in F. M. Faranda, L. Guglielmo, and A. Ianora, eds. Ross Sea ecology: Italian-tartide expeditions (1987–1995). Springer, Berlin.
- Vacchi, M., R. Williams, and M. La Mesa. 1996. Reproduction in three species of fish from the Ross Sea and Mawson Sea. Antarctic Science 8:185–192.
- Williams, R. 1985. Trophic relationships between pelagic fish and euphausiids in Antarctic waters. Pages 452–459 in SCAR Symposium on Antarctic Biology, W. R. Siegfried, P. R. Condy, Richard M. Laws, International Council of Scientific Unions, and SCAR Working Group on Biology, eds. Antarctic nutrient cycles and food webs. Springer, Berlin.
- Würzberg, L., J. Peters, H. Flores, and A. Brandt. 2011. Demersal fishes from the Antarctic shelf and deep sea: a diet study based on fatty acid patterns and gut content analyses. Deep Sea Research II 58:2036–2042.
- Zelditch, M. L., D. L. Swiderski, H. D. Sheets, and W. L. Fink. 2004. Geometric morphometrics for biologists: a primer. Elsevier, Amsterdam.