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**Research statement**

The mission of my research program is to test hypothesized mechanisms governing species richness buildup by using innovative technologies and integrative, cross-disciplinary approaches. Specifically, my research goals are to**: (1)** study the dynamics of species interactions using behavioral experiments, **(2)** quantify phenotypic diversity (e.g., morphology, diet) among fish assemblages using museum collections, and **(3)** use population genomic approaches to identify mechanisms linking micro-scale with macro-scale evolutionary processes.

A diagram of a fish

Description automatically generatedFor my research program on freshwater evolutionary ecology, I will be focusing on cichlid fishes (Family Cichlidae): one of the most species-rich families of vertebrates (Burress 2015). Within this group, Costa Rican cichlids belong to an exceptionally species-rich clade found throughout Mesoamerica (Tribe Heroini; López-Fernández et al. 2013; **Fig. 1**). Compared to the iconic adaptive radiations of East African cichlids, little research has focused on Neotropical cichlids, especially those in Costa Rica. Recent work has helped clarify the phylogenetic relationships of Neotropical cichlids, but more research is needed to test the behavioral, ecological, and evolutionary mechanisms driving diversification of this group (Říčan et al. 2016; Hauser et al. 2017; Arbour and López-Fernández 2016; Chang et al. 2019; **Fig. 1**). Greater morphological and dietary diversity concentrated in some taxa partly explains species accumulation patterns amongst clades within Neotropical cichlids (Arbour and López-Fernández 2016; Arbour et al. 2020). Still, more research is needed to further test how hypothesized mechanisms of diversity accumulation shape local diversity patterns.

**Research Goal 1:** A hallmark of cichlid radiations is their extraordinary diversity in coloration (**Fig. 2**), yet the mechanisms underlying color diversification are not well-understood. As a master’s student, I conducted field experiments aimed at testing a hypothesis for how an orange color morph within a cichlid species can be maintained at low frequencies across Nicaraguan crater lakes (Golcher-Benavides et al. 2017). As a PhD student, I was fascinated by a hypothesized mechanism of species coexistence that involved agonistic interactions biases towards intraspecific A group of fish on a white background

Description automatically generatedcoloration (Mikami et al. 2004). I conducted a field and laboratory assay to examine whether agonistic interactions can be biased against intraspecific visual cues (e.g., body coloration; Golcher-Benavides et al. 2023a *in prep.*). Our study provided the first evidence that visual cues can determine agonistic interactions. This work was conducted with help from an undergraduate student, who is also a co-author in this study and presented a poster on this research at the Virtual Evolution 2021 meeting.

**Fig. 1**: Maximum likelihood phylogeny of a representative subset of Costa Rican freshwater fish taxa. Introduced taxa are indicated with an asterisk. This molecular tree was created using the R package *rfishtree* (Chang et al. 2019).

**Fig. 2**: Cichlid fishes display a plethora of body coloration and distinct feeding strategies. Mechanisms linking body color diversity and patterns of species accumulation remain largely understudied.

At Hope College, a focus of my student-led research program will be to continue working on the mechanisms generating color diversity focused on Neotropical cichlids. Together with undergraduate students in the Biology Department at Hope College, I plan to co-develop behavioral experiments in the laboratory and in the field that test the role of visual cues in mediating key behavioral interactions (e.g., agonistic behaviors, mate choice; Golcher-Benavides et al. 2023a *in prep.*). Specifically, I plan to tackle the following questions: **1)** what role does coloration play in mate choice and behavioral isolation between species, **2)** how can behavioral biases contribute to species coexistence (i.e., reduced agonistic interactions), and **3)** how can predation influence the evolution of conspicuous signals?

I plan to incorporate a combination of laboratory and field approaches because this combined approach has been proven to be particularly powerful in providing both a degree of control and replication, while allowing for the identification of mechanisms underlying behaviors displayed in the wild. Cichlid fishes are considered ideal systems to study behavior because it is relatively straightforward to create aquarium experiments that have realistic social and physical settings to study their complex behavioral repertoire (e.g., parental care, cooperative breeding; Jordan et al. 2021). For the laboratory experiments, I plan to obtain cichlid fish from the aquarium trade. These fish can be used for both research and educational purposes, including outreach activities. I am actively involved with the American Cichlid Association and have benefitted throughout my career from the extensive knowledge and passion about cichlid biology that members of this organization display regardless of their professional background. I will partner with the Michigan Cichlid Association to participate actively in local initiatives involving local cichlid aquarium hobbyists.

**Research Goal 2:** Another celebrated feature of cichlid radiations is their dramatic diversity in feeding-related phenotypes (**Fig. 2**). This diversity is generally thought to reflect strong competition for food resources (Sturmbauer 1998). However, some cichlid communities are composed of species with minimal divergence in dietary phenotypes (i.e., shallow habitat environments in Lake Tanganyika; Golcher-Benavides et al. 2023b *in prep*). Neotropical cichlid fish assemblages found along environmental gradients provide a unique opportunity to gain mechanistic understanding of the roles ecological factors play in determining the degree phenotypic disparity in a community.

Environmental gradients represent natural experiments where we can test alternate predictions and gain insights into the complex processes that lead to the buildup of intraspecific variation necessary for speciation (Schluter and Pennell 2017). Particularly, Neotropical cichlids that are found along environmental gradients along freshwater streams and rivers in Costa Rica offer the exceptional chance to tease apart the relative contribution of the resource environment and predation pressure on phenotypic trait variability. Together with undergraduate students, I will explore the following questions: **1)** is there evidence of a species-energy relationship in cichlid fish community assembly in tropical streams, **2)** does cichlid fish phenotypic disparity vary along environmental gradients?

A diagram of a number of fish

Description automatically generated I plan to use microCT scans of Costa Rican cichlid fishes obtained at the University of Michigan’s Museum of Zoology (**UMMZ**) to conduct high-resolution shape analyses (Rolfe et al. 2020) and pair these with dietary data to determine the degree of ecological overlap among individuals in different fish communities. Through a collaboration with Dr. Hernán López-Fernández, Curator of Fishes at the **UMMZ**, Hope College’s undergraduate students will be exposed to the diversity of tropical freshwater fishes as well as the research resources at one of the world’s leading fish collections. Gaining experience working with museum specimens analyzing microCT scans could be of interest for students with a wide range of career goals, including those interested in human and veterinary medicine.

**Research Goal 3:** Why do some lineages undergo dramatic diversification whereas others do not, even when they occur in the same environment? (**Fig. 3**). Although many studies have sought to answer this question by testing how traits drive diversification rates, relatively few studies have explored links between traits, population-level processes, and macroevolutionary patterns (e.g., Singhal et al. 2019). Population-level processes are expected to influence the accumulation of diversity within a lineage because greater population structure may increase extinction risk (Jablonski 1991; Harvey et al. 2019), or conversely, provide greater opportunity for speciation (Huang 2020). To link such population-level processes to speciation, it is important to better understand the relationship between organismal traits and population-level dynamics. For example, genetic similarity within species generally decreases over space (known as isolation-by-distance). This occurs because of dispersal limitations, leading to a greater likelihood of mating between individuals that are in close spatial proximity. Lineages that show more pronounced isolation-by-distance may be more prone to undergoing allopatric speciation, which could contribute to dramatic variation in diversity across the tree of life. Dispersal limitation may result from a variety of factors, such as extrinsic environmental factors affecting animal movement, extrinsic drivers governing population growth dynamics, and/or intrinsic organismal traits limiting the probability of dispersal. Studying patterns of spatial decay in genetic similarity in both species-rich and species-poor lineages, and the extrinsic and intrinsic correlates of these spatial patterns, will help us to identify the mechanisms underlying hotspots and coldspots in biodiversity. Using a population genomics data set across 39 species of Lake Tanganyiikan cichlids, I found that population structure predicted the number of intraspecific color morphs, but this link does not ultimately translate into elevated genus-level species richness (Golcher-Benavides et al. 2023c *in prep*.; **Fig. 3**). This implies that population divergence is not the limiting step in the accumulation of species richness, consistent with emerging work in other systems (e.g., Singhal et al. 2022).

**Fig. 3**: Among Lake Tanganyikan cichlid fishes, there is substantial variation among species in the degree of spatial genetic variation detected using isolation by distance models. This figure plots the estimated value of slope for the IBD model, mapped to the tips of a species-level phylogeny. Stars indicate slopes that differ significantly from zero using Mantel tests to account for spatial autocorrelation in the data. Lineages with a high value of slope of IBD have accumulated both phenotypic and genotypic disparity while those with a low value of slope of IBD remain genetically and phenotypically homogenous. Figure replotted from Golcher-Benavides et al. 2023c *in prep*.).

Together with undergraduate students at Hope, I plan to construct a similar community-level population genomic sampling of Neotropical cichlids using increasingly affordable, genome-wide high-throughput sequencing approaches (i.e., reduced representation sequencing or low-coverage whole genome sequencing; Lou et al. 2021). I will partner with collaborators at Universidad de Costa Rica and Universidad Nacional de Costa Rica, as well as Dr. Hernán López-Fernández at **UMMZ** to collect Costa Rican cichlid fish fin clips and museum specimens along with Hope College undergraduate students. Using population genomic analyses, my students and I will calculate metrics of genetic subdivision. Understanding the links between ecological traits and genetic structure has direct implications for understanding microevolutionary processes that influence speciation and the buildup of species richness. We will then test whether: **1)** do organismal traits predict population structureand **2)** does genus-level species richness predict patterns in population genetic structure? Acquiring skills in genomic analyses at the undergraduate stage will benefit students interested in pursuing a career in data science, bioinformatics, conservation, veterinary, and/or human medicine.

My envisioned research program will allow me to return to the study of tropical freshwater fishes from my native country (Costa Rica) while continuing collaborations in the Great Lakes Region arising from my graduate studies and postdoctoral work in the United States. Over time, I would love to integrate my proposed research program into an undergraduate field course about tropical freshwater fisheries conservation in Costa Rica encompassing an experiential learning framework and opportunities for independent research. I plan to take undergraduate students to the La Selva Biological Station, where I conducted my first independent research project as an undergraduate student (Golcher-Benavides and Protti-Quesada 2011). The combination of coursework and research will enhance hands-on learning opportunities and contribute to the overarching goals of my research.

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