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Predicting speciation probability from replicated population histories

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In this issue of *Molecular Ecology*, Yamasaki et al. (2020) use genetic data from extensive sampling of *Rhinogobius* goby fish across the Ryukyu Archipelago in Japan to demonstrate the parallel speciation of a freshwater form from an ancestral amphidromous form. They then show that ecosystem size strongly predicts the probability of speciation between the two forms across islands. In doing so, this study connects population-level processes (microevolution) to broad-scale biodiversity patterns (macroevolution), an important but understudied link in evolutionary biology. Moving forward, we can build on this research to (a) more directly determine how geographic, ecological and historical factors influence the different stages of the speciation process, and (b) understand whether mechanisms inferred from insular radiations extend to those on continents, where both demographic histories and environmental regimes are likely more complex.

KEYWORDS
fish, macroevolution, parallel evolution, speciation

One of the most compelling patterns in biology is the uneven distribution of species across regions. For example, the Coral Triangle of the Indo-Pacific Ocean is home to more than 3,000 marine fish species, whereas the polar oceans are home to just tens of species (Rabosky et al., 2018). Several ecological and evolutionary hypotheses—most of which are not mutually exclusive—have been proposed to explain this heterogeneity (Schluter & Pennell, 2017). One hypothesis is that geographic variance in species diversity is due to variance in the probability of speciation; put simply, some regions have more species because speciation is more likely to occur there. Yamasaki et al. (2020) explore this hypothesis in the *Rhinogobius* goby fishes. These gobies are distributed across the Ryukyu Archipelago in Japan and consist of two forms that differ in morphology, life history, diet in the larval stage and distribution: the amphidromous migratory form and the landlocked freshwater form (Figure 1). Yamasaki et al. use a genetic data set of over 1,400 individuals from nine islands to determine how many times the freshwater form has evolved from amphidromous ancestors and then to identify the potential drivers of its repeated speciation.

Within *Rhinogobius* gobies, phenotypically similar populations occur across multiple isolated islands, leading to substantial taxonomic uncertainty. Whether freshwater populations in each island, jointly referred to as *Rhinogobius* sp. "YB," belong to the same species as the amphidromous form, *Rhinogobius brunneus*, is unclear. Yamasaki et al. used data from 20 nuclear microsatellite loci both to clarify species boundaries in this group and to test for reproductive isolation between genetically distant groups. These analyses found that the two forms correspond to distinct genetic clusters within each of the seven islands where both forms co-occur, with minimal evidence for hybridization. By genotyping individuals across morphotypes and islands, Yamasaki et al. confirmed that the two forms on each island were genetically distinct and potentially reproductively isolated.

Organisms in similar geographic and environmental settings provide unique opportunities to test whether shared ecological regimes lead to repeated evolutionary outcomes (Rosenblum & Harmon, 2011). Having demonstrated that freshwater gobies within each island are genetically distinct from the sympatric amphidromous

FIGURE 1 The two forms of *Rhinogobius* gobies from the Ryukyu Archipelago in Japan. (Top) River habitat where both forms co-occur in Iriomotejima Island. (Bottom left) A male freshwater form individual (*Rhinogobius* sp. YB) and (Bottom right) a male amphidromous form individual (*Rhinogobius brunneus*), both shown in their natural habitats. The two forms differ in both body size and colour patterning [Colour figure can be viewed at wileyonlinelibrary.com]

populations, Yamasaki et al. proceeded to test whether the freshwater forms across islands arose from a single origin or due to multiple origins. Using microsatellite data, they inferred both the phylogenetic relationships and demographic histories of the freshwater and amphidromous populations. These analyses supported the recurrent evolution of the freshwater ecotype from the amphidromous ecotype. In addition, the demographic analyses inferred gene flow during the divergence of the two forms in most of the islands. Yamasaki et al. argue this evolutionary history constitutes evidence that the freshwater form evolved via ecological speciation. Freshwater gobies spend their entire lives in rivers, where currents are strong and prey items are large, whereas the larvae of amphidromous gobies grow in the ocean, which has weaker currents and smaller prey items. Yamasaki et al. propose that differences between these two habitats create a selection gradient that may have driven divergence. These findings support that the ecotypes seen in *Rhinogobius* gobies constitute evolutionary, ecological and phenotypic replicates, suggesting that ecomorphological evolution in this system has a deterministic component.

Finally, Yamasaki et al. explore the central premise of this study: Why does speciation occur more frequently in some geographic regions than others? In the context of *Rhinogobius* gobies, why have some islands evolved the freshwater form whereas others have not? Based on both their own analyses and field surveys, Yamasaki et al. first identified on which of 18 islands the freshwater form has independently evolved from the amphidromous form. Then, they tested whether island area, catchment area, river length or number of waterfalls could predict speciation between these two forms, finding

that these four measures of ecosystem size predict speciation probability with substantial explanatory power ($r^2 > 0.5$). These results build on a number of studies from diverse organisms, which show that greater ecosystem size can lead to increased speciation (e.g. Kisel & Barraclough, 2010).

Through this set of analyses, Yamasaki et al. draw connections between population-level processes (microevolution) and broad-scale patterns of diversity (macroevolution), addressing several of the challenges in linking across these scales. For example, working taxonomies do not always accurately reflect species boundaries, particularly in rapidly radiating clades or in cases of cryptic speciation. Fuzzy species boundaries make it difficult to determine species geographic ranges and to characterize diversification dynamics, thus hampering macroevolutionary studies (Rabosky, 2016). Yamasaki et al. avoid this pitfall by delimiting putatively isolated lineages using a combination of genetic data and fine-scale geographic sampling. Second, they focus on both a narrowly circumscribed biogeographic region and phylogenetic scale, in which the processes that drive speciation are more likely to act consistently across lineages (Graham, Storch, & Machac, 2018). This is particularly true in the case of the gobies, where multiple sets of populations are independently diverging across a common ecological axis.

This study also highlights an outstanding challenge for establishing links between microevolution and macroevolution. A potential driver of diversification (here, ecosystem size) can impact diversification rates by influencing different stages of the diversification process, often in opposing directions (Harvey, Singhal, & Rabosky, 2019). For example, as Yamasaki et al. outline, larger ecosystems

can support larger populations, enabling population persistence and thus increasing speciation rates. On the other hand, larger populations are less subject to genetic drift and might be less likely to form population isolates. In other scenarios, the same driver can both increase speciation and increase extinction (Jablonski, 2008). Directly measuring rates of population persistence or isolation could help disentangle the mechanism by which these drivers influence diversification (e.g. Singhal et al., 2018). Finally, it is unclear how often diverging populations persist long enough for speciation to complete (Rabosky, 2016). In the case of the *Rhinogobius* gobies, time will tell if these young, incipient species will persist to become lasting species.

Lastly, future research can build on Yamasaki et al.'s work to address another outstanding question: Under what scenarios can we compare mechanisms inferred from different geographic contexts to inform studies of speciation? For instance, replicated ecological speciation in isolated habitats like islands and lakes has become central to the idea that evolution has a deterministic component (Losos, Jackman, Larson, Queiroz, & Rodriguez-Schettino, 1998). In agreement with this view, the results from Yamasaki et al. suggest that habitat similarity in neighbouring islands may lead to predictable evolutionary outcomes. However, it is unclear to what extent the processes that drive species and trait diversification in islands also apply to older and more diverse mainland communities (Schluter, 1988). Associations between organismal traits and lifestyle appear stronger in insular clades than continental clades (e.g. Schaad & Poe, 2010), as well as in lacustrine clades relative to riverine clades (e.g. Joyce et al., 2005). Moreover, certain demographic events like population bottlenecks and inbreeding tied to colonization may influence genetic and phenotypic divergence in island organisms more than in mainland organisms. Future studies can build on the framework introduced by Yamasaki et al. to test how geographic context determines demographic trajectories and the course of parallel evolution.

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