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6	Article type : Perspective
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9	Predicting speciation probability from replicated population histories
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16	In this issue of <i>Molecular Ecology</i> , Yamasaki et al. (2020) use genetic data from
17	extensive sampling of <i>Rhinogobius</i> goby fish across the Ryukyu Archipelago in Japan to
18	demonstrate the parallel speciation of a freshwater form from an ancestral
19	amphidromous form. They then show that ecosystem size strongly predicts the
20	probability of speciation between the two forms across islands. In doing so, this study
21	connects population-level processes (microevolution) to broad-scale biodiversity
22	patterns (macroevolution), an important but understudied link in evolutionary biology.
23	Moving forward, we can build on this research to (1) more directly determine how
24	geographic, ecological, and historical factors influence the different stages of the
25	speciation process, and (2) understand whether mechanisms inferred from insular
26	radiations extend to those on continents, where both demographic histories and
27	environmental regimes are likely more complex.
28	One of the most compelling patterns in biology is the uneven distribution of species
29	across regions. For example, the Coral Triangle of the Indo-Pacific Ocean is home to more than
30	3,000 marine fish species, whereas the polar oceans are home to just tens of species (Rabosky
31	et al. 2018). Several ecological and evolutionary hypotheses - most of which are not mutually
32	exclusive - have been proposed to explain this heterogeneity (Schluter & Pennell 2017). One
	This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the <u>Version of Record</u> . Please cite this article as <u>doi:</u> 10.1111/MEC.15577

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33 hypothesis is that geographic variance in species diversity is due to variance in the probability of 34 speciation; put simply, some regions have more species because speciation is more likely to 35 occur there. Yamasaki et al. (2020) explore this hypothesis in the *Rhinogobius* goby fishes. 36 These gobies are distributed across the Ryukyu Archipelago in Japan and consist of two forms 37 that differ in morphology, life-history, diet in the larval stage, and distribution: the amphidromous 38 migratory form and the landlocked freshwater form (Fig. 1). Yamasaki et al. use a genetic 39 dataset of over 1,400 individuals from nine islands to determine how many times the freshwater 40 form has evolved from amphidromous ancestors and then identify the potential drivers of its 41 repeated speciation.

42 Within Rhinogobius gobies, phenotypically similar populations occur across multiple 43 isolated islands, leading to substantial taxonomic uncertainty. Whether freshwater populations in 44 each island, jointly referred to as *Rhinogobius* sp. "YB", belong to the same species as the 45 amphidromous form, Rhinogobius brunneus, is unclear. Yamasaki et al. used data from 20 46 nuclear microsatellite loci to both clarify species boundaries in this group and to test for 47 reproductive isolation between genetically distant groups. These analyses found that the two 48 forms correspond to distinct genetic clusters within each of the seven islands where both forms 49 co-occur, with minimal evidence for hybridization. By genotyping individuals across 50 morphotypes and islands, Yamasaki et al. confirmed that the two forms on each island were 51 genetically distinct and potentially reproductively isolated.

52 Organisms in similar geographic and environmental settings provide unique 53 opportunities to test whether shared ecological regimes lead to repeated evolutionary outcomes 54 (Rosenblum & Harmon 2011). Having demonstrated that freshwater gobies within each island 55 are genetically distinct from the sympatric amphidromous populations, Yamasaki et al. 56 proceeded to test if the freshwater forms across islands arose from a single origin or due to 57 multiple origins. Using microsatellite data, they both inferred the phylogenetic relationships and 58 demographic histories of the freshwater and amphidromous populations. These analyses 59 supported the recurrent evolution of the freshwater ecotype from the amphidromous ecotype. In 60 addition, the demographic analyses inferred gene flow during the divergence of the two forms in 61 most of the islands. Yamasaki et al. argue this evolutionary history constitutes evidence that the 62 freshwater form evolved via ecological speciation. Freshwater gobies spend their entire lives in 63 rivers, where currents are strong and prey items are large, whereas the larvae of amphidromous 64 gobies grow in the ocean, which has weaker currents and smaller prey items. Yamasaki et al. 65 propose that differences between these two habitats create a selection gradient that may have 66 driven divergence. These findings support that the ecotypes seen in *Rhinogobius* gobies

67 constitute evolutionary, ecological, and phenotypic replicates, suggesting that ecomorphological68 evolution in this system has a deterministic component.

69 Finally, Yamasaki et al. explore the central premise of this study: why does speciation 70 occur more frequently in some geographic regions than others? In the context of Rhinogobius 71 gobies, why have some islands evolved the freshwater form whereas others have not? Based 72 on both their own analyses and field surveys, Yamasaki et al. first identified on which of 18 73 islands the freshwater form has independently evolved from the amphidromous form. Then, they 74 tested if island area, catchment area, river length, or number of waterfalls could predict 75 speciation between these two forms, finding that these four measures of ecosystem size predict 76 speciation probability with substantial explanatory power ( $r^2 > 0.5$ ). These results build on a 77 number of studies from diverse organisms showing that greater ecosystem size can lead to 78 increased speciation (e.g., Kisel & Barraclough 2010).

79 Through this set of analyses, Yamasaki et al. draw connections between population-80 level processes (microevolution) and broad-scale patterns of diversity (macroevolution), 81 addressing several of the challenges in linking across these scales. For example, working 82 taxonomies do not always accurately reflect species boundaries, particularly in rapidly radiating 83 clades or in cases of cryptic speciation. Fuzzy species boundaries make it difficult to determine 84 species geographic ranges and to characterize diversification dynamics, thus hampering 85 macroevolutionary studies (Rabosky 2016). Yamasaki et al. avoid this pitfall by using their 86 genetic data across their fine-scale geographic sampling to delimit putatively isolated lineages. 87 Second, they focus on both a narrowly circumscribed biogeographic region and phylogenetic 88 scale, in which the processes that drive speciation are more likely to act consistently across 89 lineages (Graham et al. 2018). This is particularly true in the case of the gobies, where multiple 90 sets of populations are independently diverging across a common ecological axis.

91 This study also highlights an outstanding challenge for establishing links between 92 microevolution and macroevolution. A potential driver of diversification (here, ecosystem size) 93 can impact diversification rates by influencing different stages of the diversification process, 94 often in opposing directions (Harvey et al. 2019). For example, as Yamasaki et al. outline, larger 95 ecosystems can support larger populations, enabling population persistence and thus 96 increasing speciation rates. On the other hand, larger populations are less subject to genetic 97 drift and might be less likely to form population isolates. In other scenarios, the same driver can 98 both increase speciation and increase extinction (Jablonski 2008). Directly measuring rates of 99 population persistence or isolation could help disentangle the mechanism by which these 100 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.

104 Lastly, future research can build on Yamasaki et al.'s work to address another 105 outstanding question: under what scenarios can we compare mechanisms inferred from 106 different geographic contexts to inform studies of speciation? For instance, replicated ecological 107 speciation in isolated habitats like islands and lakes has become central to the idea that 108 evolution has a deterministic component (Losos et al. 1998). In agreement with this view, the 109 results from Yamasaki et al. suggest that habitat similarity in neighboring islands may lead to 110 predictable evolutionary outcomes. However, it is unclear to what extent the processes that 111 drive species and trait diversification in islands also apply to older and more diverse mainland 112 communities (Schluter 1988). Associations between organismal traits and lifestyle appear 113 stronger in insular clades than continental clades (e.g., Schaad & Poe 2010), as well as in 114 lacustrine clades relative to riverine clades (e.g., Joyce et al. 2005). Moreover, certain 115 demographic events like population bottlenecks and inbreeding tied to colonization may 116 influence genetic and phenotypic divergence in island organisms more than in mainland 117 organisms. Future studies can build on the framework introduced by Yamasaki et al. to test how 118 geographic context determines demographic trajectories and the course of parallel evolution.

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## 120 Figures

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 color patterning.

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