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## update

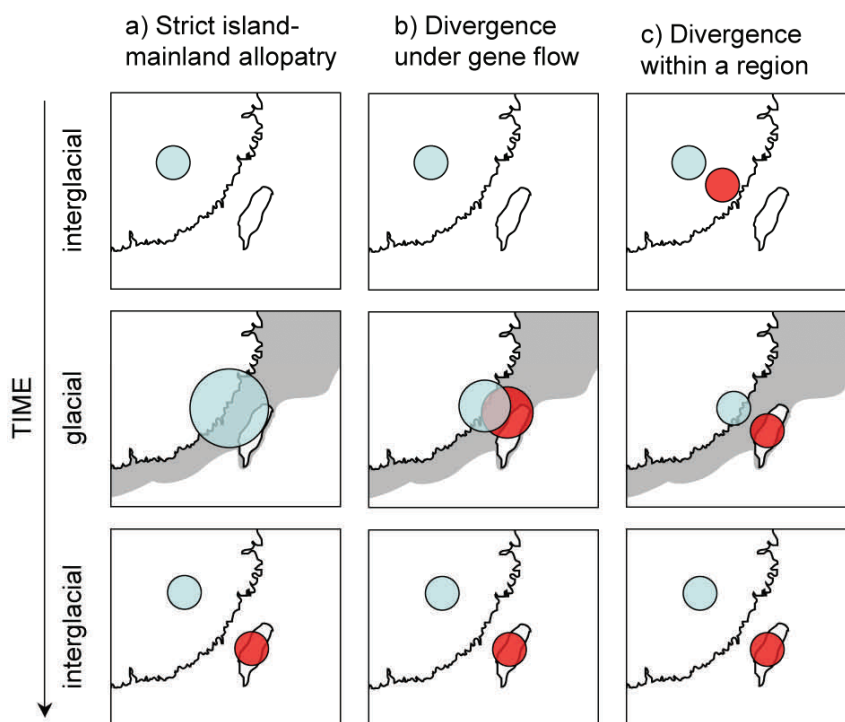
## Divergence of island biotas when they were not always islands

Islands have frequently captured the attention of biogeographers, providing insights into oceanic dispersal capabilities (McDowall 2002), the processes of adaptation and diversification (Darwin 1872, Losos and Ricklefs 2009), and immigration-extinction dynamics (MacArthur and Wilson 1967). Furthermore, the presence of related but distinct lineages on islands and continents is considered to represent classic examples of allopatric speciation (Mayr 1942). However, for continental shelf islands—those that possessed terrestrial connections to other landmasses via exposed continental shelf during low sea stands (Whittaker and Fernández-Palacios 2007)—the interpretation may not always be so simple.

Continental shelf islands are common throughout the globe, ranging from the numerous small nearshore islands that dot our coastlines, to larger and more notable examples, represented by places such as Tasmania, New Guinea, Borneo, Sri Lanka, Taiwan, Japan, England and the Falkland Islands (Malvinas). Continental shelf islands, like oceanic islands, often house a variety of endemic

species (Kallimanis et al. 2010), and divergence resulting from the development of island-mainland allopatric distributions is typically invoked (Fig. 1a). However, continental shelf islands have repeatedly and predominantly experienced terrestrial connections to mainlands throughout the Pleistocene, represented by glacial low sea stands (Lambeck et al. 2002). Therefore, the divergence of continental shelf island biotas from those on the mainland may have occurred by various means (allopatric, peripatric, parapatric or sympatric speciation; Coyne and Orr 2004) prior to the development of island-mainland allopatric distributions themselves (e.g. Fig. 1b,c).

A recent study from Taiwan illustrates a novel approach by which the divergence of sister lineages can be tested for deviation from a strictly allopatric island-mainland model. Li *et al.* (2010a) studied Taiwanese and Chinese hwamei (*Leucodioptron taewanus* and *L. canorum canorum*, respectively), representing species of babbler that are sedentary and occupy the margins of secondary broadleaf evergreen woodlands.



**Figure 1.** Hypothetical divergence scenarios leading to contemporary island-mainland sister-lineages. Circles of different colours indicate the geographic distribution of diverging lineages. The grey shaded areas indicate continental shelf exposed during Pleistocene glaciations between China and the continental shelf island of Taiwan. (a) Strict island-mainland allopatric divergence. Island and mainland populations of a widespread ancestor were isolated following a marine transgression. (b) Divergence under gene flow. Divergence of lineages occurred despite sympatry or parapatry and gene flow, with island-mainland allopatric distributions formed subsequently. (c) Divergence of lineages within a region (allopatric within the mainland, in this case), with island-mainland allopatry formed subsequently.

These species are unlikely candidates for marine dispersal, but movement between Taiwan and China may have been achieved by their ancestors during Pleistocene low sea stands, when the Taiwan Strait was emergent (Fig. 1). Consequently, divergence of these lineages may have proceeded under an alternate geographic scenario.

Li *et al.* (2010a) documented DNA sequence variation at a large number of independent nuclear markers (18 loci), and employed these data to test hypotheses regarding the demographic history of lineages using weighted-regression-based approximate Bayesian computations. Two models of lineage divergence were compared for the hwamei. The first represented divergence under strict allopatry (without subsequent gene flow), akin to a single colonisation (founder) event, or vicariant isolation of populations (Fig. 1a). The alternate model allowed gene flow for a period subsequent to the initiation of lineage divergence, consistent with divergence under parapatry or sympatry and interbreeding (Fig. 1b). Coalescent simulations were performed under these models, and 11 summary statistics were calculated for each simulated 18-locus dataset (e.g. number of polymorphic sites, haplotype diversity, nucleotide diversity,  $F_{ST}$ , number of polymorphisms that are shared, unique, or fixed between lineages). The summary statistics from simulated datasets were then compared against those from the empirical data. The non-allopatry (gene flow following divergence) model better explained the observed data than the strict allopatry model. A large time discrepancy was also observed between the initiation of lineage divergence (3.47 Mya) and cessation of gene flow (0.52 Mya).

The estimates of total lineage divergence time, and time for cessation of gene flow, raise two interesting questions regarding the geographic distributions of these lineages during their divergence (assuming that these time estimates are not strongly influenced by potential errors with the molecular clocks). Firstly, although a model involving gene flow between lineages during the early stages of their divergence was favoured, the mid-Pliocene was characterised by

elevated sea levels (Raymo *et al.* 2011), and therefore divergence must have been occurring within either Taiwan or China, and not across both. Secondly, as a population of *L. c. canorum* artificially introduced to Taiwan can interbreed with *L. taiwanus* (Li *et al.* 2010b), the cessation of gene flow 0.52 Mya must represent the formation of an ongoing allopatric distribution. Li *et al.* (2010a) looked to paleovegetation reconstructions and the presence of unsuitable hwamei habitat (savannah) across the Taiwan Strait during the last glacial period as a potential explanation for a lack of more recent gene flow. Regardless, the formation of an allopatric island-mainland distribution appears only to have interrupted gene flow between lineages that were already diverging in parapatry or sympatry.

The above example highlights the potential complexities of historical divergence between continental shelf island and mainland populations. Such complexity may owe to the geographically peripheral location of continental shelf islands, placing them ideally to sequester variants that developed in a mainland species (e.g. Fig. 1c). Regardless, allopatric island-mainland divergence of lineages should not be assumed for continental island biotas, and further research is required to examine the prevalence of alternate divergence scenarios. The same could also be said for other systems where allopatric divergence is typically invoked (e.g. oceanic islands); instead, divergence may have occurred during periods of on-going gene flow ("soft vicariance"; Hickerson and Meyer 2008), or preceded the attainment of contemporary allopatric distributions.

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## update

# Escaping the trap of low sample size in island biogeography

Ecologists and evolutionary biologists have been fascinated by island biodiversity at least since the first travels of 18<sup>th</sup> century naturalists. Islands' sometimes exuberant diversity – full of rare forms and endemic species or varieties – their character of discrete entities and their isolation from the mainland make islands exceptional natural laboratories for the development of ecological and evolutionary theory. Perhaps unsurprisingly, they have been home to many major theoretical advances in these disciplines during the last 50 years (see Whittaker & Fernández-Palacios 2007), from which the seminal Equilibrium Theory of Island Biogeography (ETIB, MacArthur and Wilson 1967) is just the most outstanding example.

In spite of the importance of islands and archipelagos for the development of biogeographical theory, the stubborn persistence of archipelagos and island groups to come in low island numbers and the tendency of different

characteristics to be collinear makes it difficult to evaluate hypotheses and extract conclusions about the processes originating from the diversity and structure of their assemblages. For example, finding a significant relationship (at the 0.05 level) between any two island descriptors for the seven main islands of the Canarian archipelago using simple least-squares regression models requires percentages of explained variation (adjusted  $r^2$ ) of about 50%. This problem is further aggravated when working with patterns of within-island diversification, because many islands may be too small to host speciation processes (see e.g. Losos & Schluter 2000), therefore reducing the number of islands that can be used for these particular analyses in each archipelago. Needless to say, discriminating between three or four non-mutually exclusive hypotheses represented by predictors with different degrees of collinearity is typically a difficult task in island biogeography.