

## Forum

### How does speciation in marine plankton work?

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**Marine plankton species are ecologically important, yet, it remains unclear how they originate in the ocean, where few barriers are apparent to cause the most common type of speciation – divergence in isolation. Here I discuss the use of modern evolutionary genetic approaches to shed light on longstanding questions regarding their evolution.**

#### Introduction

The ecological significance of marine plankton makes it important to understand the evolutionary processes underpinning their biodiversity and ability to adapt to a changing environment (e.g., [1,2] and references therein). While phenotypic or ecological outcomes of plankton adaptation have been studied to some extent, relatively little is known about evolutionary genetic processes underlying their adaptation and speciation [1]. As the nature of ‘species’ in prokaryotes is different from that in eukaryotes, the discussion below is focusing on pelagic marine eukaryotic protists, referred to as ‘plankton’ for brevity.

Due to a lack of apparent geographic barriers in the open ocean, the predominance of allopatric speciation in the marine realm has long been questioned [3,4] and multiple examples of coexisting marine sibling species suggest that marine speciation is frequently sympatric, that is, driven by adaptation to different ecological niches in the same geographic location. Yet, the work in terrestrial organisms shows

that sympatric speciation is relatively uncommon [5]. However, microevolutionary processes – the very foundation of evolutionary change – may work in rather different ways in relatively small populations of terrestrial organisms and astronomically large populations of marine plankton [1,6]. Currently we lack understanding of microevolutionary processes in such enormous populations, which is well illustrated by the extreme disparity between theoretical expectations and actual values of genetic diversity in marine plankton [6]. Population size is one of the most important parameters that determines how natural selection works. Given the very large census and effective population sizes in pelagic eukaryotic microbes, natural selection is expected to be very powerful [1], which may facilitate sympatric speciation. If sympatric speciation is indeed playing a significant role in origination of pelagic marine organisms, it would sharply contrast with the terrestrial realm, where geographic isolation is thought to be a major driver of speciation [5].

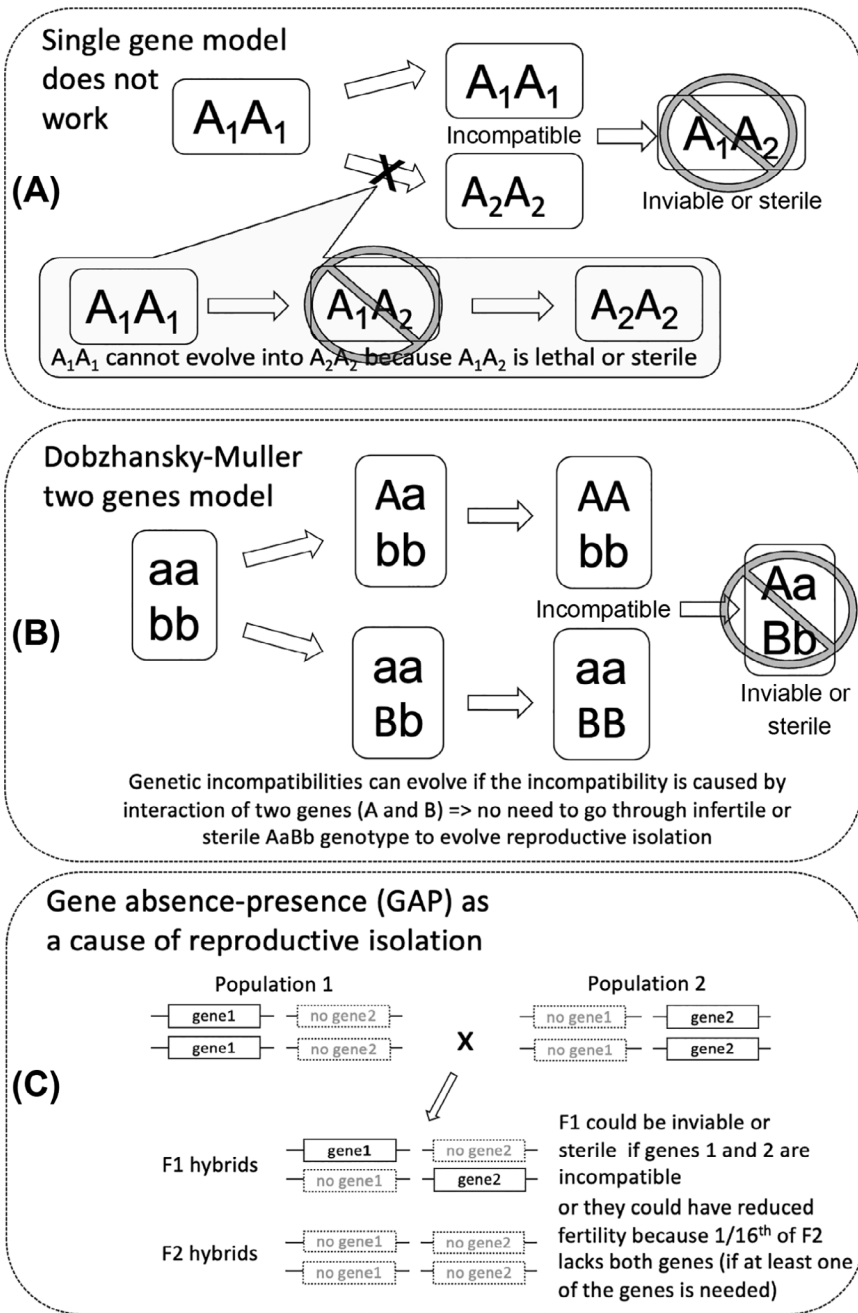
Evolution of reproductive incompatibilities (RI) is a key step in speciation, which is thought to typically follow the classic ‘Dobzhansky–Muller’ (DM) model [5]. According to the DM model, a new mutation causing RI with the rest of the population cannot spread because it is highly deleterious in heterozygotes (Figure 1A); thus, the spread of at least two mutations is required for evolution of RI (Figure 1B). Separately, these mutations are neutral, but are lethal or strongly deleterious, due to transregulatory interactions, when brought together in hybrids. DM-like gene misregulation in hybrids may be particularly important in the context of gene absence/presence (GAP) variation in marine planktonic protists, if a significant part of their pangenome is ‘accessory’, as was reported for coccolithophore *Emiliana huxleyi* [7], but remains to be tested in other plankton groups. Having different sets of accessory genes present may make individuals of

the same species reproductively incompatible (Figure 1C) and may lead to speciation if the incompatible genotypes spread to high frequency via clonal expansion, hitchhiking, or genetic drift. The spread of incompatible genotypes in the same or different geographic locations would lead to sympatric or allopatric speciation, respectively. The importance of GAP and genomic structural variation (SV) in adaptation and speciation is actively discussed in the literature (e.g., [8] and other papers in the same special issue) and their roles in speciation have been recently reviewed [9], but not in the context of marine eukaryotic microbes.

#### Evolutionary genetic approaches

The level and patterns of genetic diversity within the same species and their comparisons to closely related species are highly informative about many aspects of evolutionary process, including adaptation and speciation (e.g., [10]). For example, they can be used to ‘scan’ for genes evolving under positive selection within a species [11] or to infer past demographic history – the variation of population size through time [12]. To study microevolutionary processes underpinning plankton speciation in the open ocean, it is possible to use various approaches ranging from simple descriptive statistics, such as  $F_{st}$  that characterises the extent of population differentiation, to population genetic modelling of the most likely speciation scenarios [10], such as implemented in *fastsimcoal* [13]. Even the simple descriptive statistics can help to test specific hypotheses, such as the role of GAP and accessory regions in speciation. In particular, it is possible to test whether genetic differentiation between populations or nascent species is higher in the GAP regions compared to that elsewhere in the genome.

The evolutionary genetic modelling approaches (e.g., [13]) are quite powerful and informative about the process of speciation. For example, to study whether the species hybridize or have entirely separate



**Figure 1. Evolution of reproductive incompatibilities between nascent species.** (A) A model with a single gene causing reproductive isolation does not work because the intermediate step to go from  $A_1A_1$  to  $A_2A_2$  – the heterozygote  $A_1A_2$  – is infertile or sterile. (B) A model with two genes, each mutating and spreading in a separate population – the Dobzhansky-Muller (DM) model – does work as it does not go through the inviable  $AaBb$  to evolve species incompatibilities. (C) A diagram illustrating how gene absence-presence polymorphisms could lead to reproductive isolation.

gene pools, one can test whether a model allowing for interspecific gene flow fits data significantly better than the 'null' model without gene flow. The fit of these and other scenarios to data can be compared with maximum likelihood ratio tests, allowing us to test whether inclusion of gene flow (or other parameters) in the model makes it significantly more realistic. Furthermore, the estimates of specific parameters, such as the extent of gene flow between the species, the timing of speciation, population sizes of the ancestral and derived species etc., make it possible to reconstruct a realistic scenario of speciation (e.g., [10]). For example, the allopatric speciation scenario implies isolation (no gene flow) of nascent species right after the species split by a geographic barrier, possibly followed by some gene flow once the ranges of the two species overlap later on (secondary contact). By contrast, under sympatric or parapatric speciation scenarios, we would expect to see initially high, but gradually reducing, gene flow following the species split [5].

Isolating mechanisms splitting an ancestral species into separate gene pools can be classified into extrinsic – such as physical or geographic barriers to gene flow – and intrinsic – such as genetic incompatibilities between nascent species [14]. The relative contributions of extrinsic and intrinsic isolation mechanisms to speciation in marine plankton is little studied. In order to identify the intrinsic 'speciation genes' that likely play a role in genetic isolation of the closely related species it is possible to use genome scans for 'outlier' loci with greater than expected differentiation between species or diverging populations, such as implemented in *Bayescan* [15]. While a number of speciation genes were identified in *Drosophila* and some other terrestrial organisms [5], very little is known about such genes in marine eukaryotic microbes. Similar scans for highly differentiated genes can be conducted within species for diverging populations

Trends in Microbiology

or populations inhabiting contrasting conditions (e.g., Arctic versus temperate), with high-differentiation outliers likely corresponding to genetic variants involved in adaptation to local conditions.

### Recent genome-wide analyses of speciation in marine plankton

The evolutionary genetic approaches mentioned above are starting to be applied to marine plankton. The analyses of genetic variation along the environmental gradients, such as studies of *Skeletonema marinoi* in the Baltic sea salinity gradient, or *Fragilariopsis kerguelensis* in the latitudinal transect across the Southern ocean ([1,2] and references therein), are informative about local adaptation that may lead to speciation. The correlations of genetic relatedness with local environmental variables rather than distance and geographic location for *Thalassiosira rotula* [4] suggested a stronger role for ecological selection rather than physical barriers in structuring of plankton populations. However, the analysis of multiple speciation events in the coccolithophore genus *Gephyrocapsa* [10] indicated the importance of physical barriers as the causes of isolation driving speciation. Physical barriers, such as marine or ocean fronts, do exist in the open ocean, but it remains unclear whether they can ensure divergence of populations separated by a front. Ocean fronts are likely quite porous barriers to gene flow, but even a porous barrier can promote speciation if it reduces gene flow ( $m$ ) to  $m \ll 1/N_e$ , where  $N_e$  is the effective population size [5].

The model-based evolutionary genetic analyses of multiple *Gephyrocapsa* genomes revealed that speciation events in this genus coincided with the cold phases

of the consecutive glaciation cycles in the last 0.6 MY [10], suggesting that during the ice ages the conditions in the oceans promote new species formation. It is interesting to speculate that polar fronts moving closer to the equator during the ice ages may act as geographic barriers isolating plankton populations in different basins, causing their divergence and speciation. A lower sea level during the ice ages may also contribute to isolation of marine populations by turning shallow straights into land bridges separating previously connected water basins. Furthermore, the changes in water column stratification and ocean circulation during glacial periods may promote stronger segregation of ecological niches, driving isolation and speciation in populations of marine plankton [10]. As such, repeated glaciations in the glacial cycles may act as a 'speciation pump' for marine plankton.

Extension of this work to a wider set of marine plankton species will help to shed light on evolutionary processes underpinning biodiversity of eukaryotic microbes in world oceans. Furthermore, integrated analyses of genome sequence and fossil data are possible in microbes with hard shells or skeletons, such as calcifying foraminifera and coccolithophores (e.g., Figures 2C–F in [10]). Such integrated analyses of fossil and genetic data provide a powerful tool to reveal the evolutionary genetic processes that underly the macro-evolutionary patterns detectable in the fossil record.

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### Declaration of interests

No interests are declared.

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