

Evolution and stability of ring species

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Neutral models, in which genetic change arises through random variation without fitness differences, have proven remarkably successful in describing observed patterns of biodiversity, despite the manifest role of selection in evolution. Here we investigate the effect of barriers on biodiversity by simulating the expansion of a population around a barrier to form a ring species, in which the two ends of the population are reproductively isolated despite ongoing gene flow around the ring. We compare the spatial and genetic properties of a neutral agent-based population model to the greenish warblers' complex, a well-documented example of an actual ring species in nature. Our results match the distribution of subspecies, the principal components of genetic diversity, and the linear spatial–genetic correlation of the observed data, even though selection is expected to be important for traits of this species. We find that ring species are often unstable to speciation or mixing but can persist for extended times depending on species and landscape features. For the greenish warblers, our analysis implies that the expanded area near the point of secondary contact is important for extending the duration of the ring, and thus, for the opportunity to observe this ring species. Nevertheless it also suggests the ring will break up into multiple species in 10,000 to 50,000 y. These results imply that simulations can be used to accurately describe empirical data for complex spatial–genetic traits of an individual species.

geography | topopatric | allopatric | birds | DNA

There is a growing paradox in our understanding of the core issues of speciation and biodiversity. First, the manifest empirical importance of selection in the traits of species appears to be counter to the ability to describe biodiversity by using neutral models of speciation (1–4). Second, geographical heterogeneity, including geographical isolation, is no longer considered necessary to account for the emergence of new species. Traditionally, the emergence of new species has been explained by a period of geographic isolation of subpopulations. In the absence of gene flow, genetic differences accumulate and reproductive isolation eventually arises (5). However, if population ranges are large enough, genetic divergence can lead to speciation despite ongoing gene flow (6), as demonstrated by empirical and theoretical results (7–15). Moreover, it has been shown that existing patterns of diversity are consistent with such speciation with ongoing gene flow and without trait selection or spatial heterogeneity, as long as mating is constrained by spatial and genetic distances (15). Here we show that neutral models of speciation can also account for the genetic diversity of a single species in a context in which geographical barriers play a central role in that diversity. We compare the diversity of a neutral model to empirical findings about a ring species formed when population expansion occurred around a geographical barrier. The genetic patterns are consistent even though selection is expected to be important for traits of this species (11, 16, 17).

Currently, the best documented example of a ring species is that of the greenish warblers, which inhabit a ring around the Tibetan Plateau (11). In the northernmost area of this ring are two Siberian taxa that are reproductively isolated and occupy overlapping geographical regions (18). Gene flow is still possible between them over multiple generations through a chain of reproductively linked taxa around the ring. One noteworthy char-

acteristic is that the Siberian taxa, which occur in the area of secondary contact (i.e., ring closure) of the expanding population, have much larger distribution ranges than do other subspecies. The correlation between range size and latitude is a strong pattern found in many terrestrial groups of the Old World (19).

We simulated the formation of a ring species (Fig. 1) (20), explicitly including the ring topography and allowing a small initial population to grow as it expands and differentiates around a geographical barrier (Fig. S1). We used an individual-based model based on neutral replacement with local mating, migration, and mutation (*Methods*). Reproductive isolation is modeled by a multilocus generalization of the Bateson–Dobzhansky–Muller model whereby the population evolves through nearly constant fitness ridges (21, 22). The initial population is set within a starting area, and the individuals whose local mating area is underpopulated generate two rather than one offspring before dying. This enables the population to grow and spread up to the carrying capacity of the entire available space.

Results and Discussion

The genetic variation plot (Fig. 1 *C* and *D*) reveals a gradual genetic change over geographical space (see also Figs. S2 and S3). Simulated and actual warbler populations have a similar decomposition of variance (15.9% vs. 19.4% for the first principal component and 10.8% vs. 5.6% for the second principal component, respectively). The genetic distance between individuals increases linearly with their geographic distance as measured around the ring in both cases (Fig. 1 *E* and *F*). Different behaviors are expected for a single mixed species or multiple species (Fig. S4). For the sampling shown in Fig. 1, the average genetic distance within populations—the number of differing loci along their strings—is approximately three and the genetic distance between the populations at the area of secondary contact is approximately seven. This is in agreement with amplified fragment length polymorphism (AFLP) data (11) in which AFLP distances between populations at secondary contact is approximately twice the average distance within populations. The number of genetic differences in the sampled model corresponds to the same proportion of AFLP differences in the sampled experimental observations. This indicates that populations separated by half the ring's length should already be reproductively isolated. The terminal populations came into contact after ~2,000 generations (Fig. 2, middle line). The number of generations is consistent with the timing of habitat recovery as a result of tree cover expansion—an important factor in the spread of the greenish warbler. The forest range expanded starting approximately 10,000 y ago and achieved its current area ~2,000 y later (17). Given the greenish warblers' annual life cycle and assuming that their range expansion accompanied this forest recovery (19), the rates of population expansion in our simulations coincide, consistent with empirical

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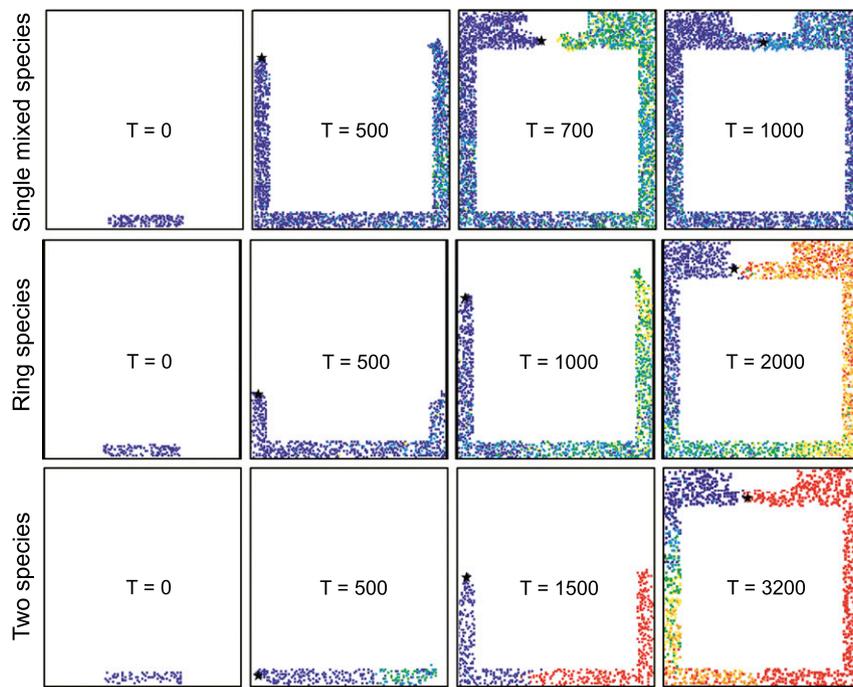


Fig. 2. Three simulations of population expansion around a geographical barrier resulting in single species, ring species, and multiple species. Snapshots from *Left to Right* show the time evolution of the simulated populations as they expand (T is the number of generations) for different values of carrying capacity K and dispersal rate D . (*Right*) Population a few hundred generations after secondary contact. Colors represent genetic distance to a reference individual marked as a star. Single species (*Top*): $K = 3,600$ and $D = 0.3$. Ring species (*Middle*): The same simulation shown in Fig. 1, $K = 2,400$ and $D = 0.15$. Multiple species (*Bottom*): $K = 1,500$ and $D = 0.1$; two completely reproductively isolated groups are present after 1,500 generations. At $T = 3,200$, genetic variation can be seen on the left in the color variation but not on the right, as all individuals on the right are incompatible with the starred individual, and therefore are marked as red.

range expansion and genetic differentiation will determine the fate of the terminal populations when they come into secondary contact. Increasing carrying capacity decreases differentiation (32) and increases the velocity. Other features that affect this interplay include population features (e.g., growth rate, mating distance, dispersal rate, and mobility) and landscape features (e.g., corridor width, distance around the barrier). None of these provides stability for a ring species. We tested the robustness of ring species formation to variation in the geographical structure

of the ring. We hypothesized that the larger habitable area present near the region of secondary contact enhanced the likelihood of ring species formation. Larger populations of the divergent types inhibit genetic fluctuations that could lead to mating opportunities that would revert the speciation process (33). Simulations confirmed that when the excess area was displaced to a different location in the ring near the point of origin, equivalent to shifting the point of origin from south to north, ring species were less likely to form, even though the time until secondary

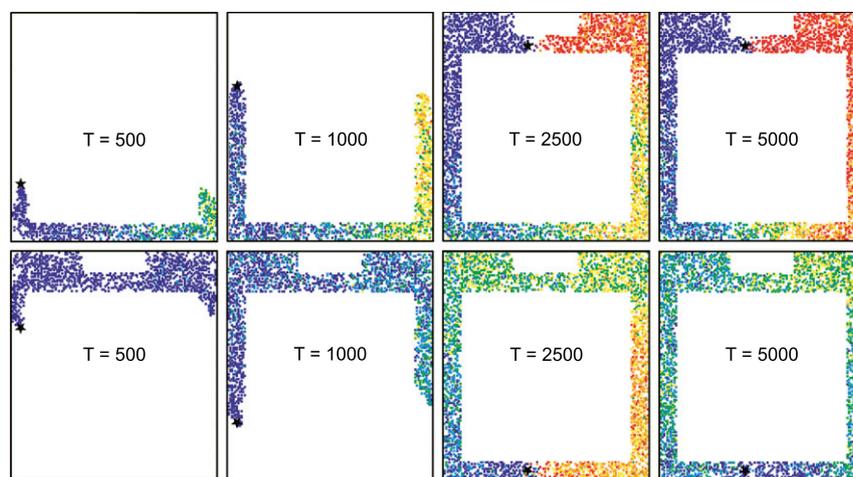


Fig. 3. Spatial snapshots showing expansion of simulated populations around a ring. *Upper* and *Lower* images differ only in the place of origin of the expanding population, south and north, respectively. As there are larger habitable areas in the north, the *Upper* simulation has this larger area at the point of secondary contact, and the *Lower* has it near the point of origin. Simulation parameters are $K = 3,300$ (carrying capacity) and $D = 0.1$ (dispersal rate). Colors represent the genetic distance to a reference individual marked as a star.

individuals (Fig. S1). The remaining sites can be occupied by multiple individuals. The carrying capacity, K , determines the maximum population size allowed in the entire population. The expected demographic density, ρ , is calculated as the ratio between K and the number of available sites. The initial population consists of genetically identical individuals randomly placed in a fixed area below the larger barrier, as shown in Fig. S1. The number of individuals in the initial population is given by ρ times the number of sites in this area.

The population evolves in discrete generations. Each individual seeks potential mates for reproduction once and is replaced by the resulting offspring. However, there is a probability Q that the individual will not reproduce at all. In this case, a neighbor is selected at random to reproduce in its place. In each reproductive event, one individual is selected at random from the list of potential mates (meeting spatial and genetic criteria), and the genetic information of both parents is combined with one genetic crossover for which the breakpoint is randomly selected along the string. There is a mutation rate per locus, μ . Offspring dispersal occurs with probability D ; the offspring is placed at one of the 20 neighboring sites, chosen randomly. In addition, if the demographic density in the mating area is lower than 60% of the expected demographic density, ρ , a second offspring is produced. This allows for the spreading of the population toward empty areas, as shown in Fig. 3 and Fig. S2. After the population reaches the carrying capacity, each individual can have only one offspring. If there are fewer than P potential mates for a specific individual, the mating area for that individual is increased by setting S to $S + 1$. If the number of available mates is still smaller than P , the process is repeated. S may be increased by a maximum of 10 units, in which case, if there are still less than P potential mates, a neighbor is randomly selected to reproduce instead. A highly divergent individual is likely to be replaced by a more common type. This selects against rare types when they coexist with a common type in a geographical region.

For the results reported, B is equal to 125, S is 9, G is 20, μ is 0.0003, Q is 0.3, P is 20, and the geographical barriers occupy 11,796 of 18,176 sites, leaving 6,380 available (Fig. S1).

A species is identified as a group of organisms that are connected by gene flow and separated from all others by the genetic restriction on mating determined by G . This definition does not require all members of a species to be able to mate with each other; two members can be incompatible, as long as they can exchange genes indirectly through other members of the species. As an example, three individuals A , B , and C whose genetic distances satisfy $d(A,B) < G$, $d(B,C) < G$, but $d(A,C) > G$ belong to the same species. A mutation occurring in A can be transmitted to the offspring of A and B that can, in turn, pass the mutation on when mating with C or its offspring. Considering this strategy to delimitate species, ring species are identified as a population in which we would identify two species when considering only the individuals located in the area of secondary contact (Fig. S1), but a single species when considering the population as a whole.

In all figures in which individuals are shown in color, the color is according to the genetic distance to a reference individual, marked as a star. Dark blue corresponds to potential mates for the reference individual (those whose genetic distance is less than the critical value, G). The remaining colors represent genetic distances in the following intervals: light blue (G , $1.15G$); green ($1.15G$, $1.15^2 G$); yellow ($1.15^2 G$, $1.15^3 G$); orange ($1.15^3 G$, $1.15^4 G$); and red, greater than or equal to $1.15^4 G$. Ring species formation is sensitive to variations in S , G , μ , K , and D . The effects of varying K and D are described in the text and figures; varying other parameters combinations yield qualitatively similar results.

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