Migration and the Origin of Species

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Introduction

The earth is inhabited by a breathtaking number of different species. Currently, 1.7 million species have been described by scientists, and the number of undescribed species is expected to exceed this figure by at least one order of magnitude. All living and extinct species derive from a common ancestor, and the process by which an existing species gives rise to new species is called *speciation*. Understanding speciation is one of the defining problems in evolutionary biology. Although Charles Darwin named his seminal book "On the Origin of Species" (1859), he actually did not develop a theory of speciation but rather derived how evolutionary change ensues from the occurrence of heritable variation and natural selection. It was only during the "modern synthesis" of the 1930s that evolutionary biologists developed a clearer picture of the speciation process. The early ideas put a strong emphasis on the role of migration in speciation. Especially Ernst Mayr (1942) pushed the idea that speciation requires the split of an ancestral population into two or more spatially isolated subpopulations, which then evolve to become distinct species. Mayr's reasoning was that migration and subsequent interbreeding between immigrants and residents result in the exchange of genetic material. This exchange tends to homogenize the two subpopulations and therefore counteracts divergence and speciation. In this chapter, I will refer to migration in subdivided population as gene flow because this term directly refers to the biological relevant effect of migration in sexually reproducing plant and animal populations. Although still prominent, Mayr's strict view is not as dominant as it used to be, and nowadays the possibility of speciation in the presence of gene flow is supported both by empirical evidence and by mathematical models. In this chapter, I will give an overview of speciation theories with an emphasis on the role of gene flow.

The structure of this chapter is as follows. In the next section, I discuss some difficulties in defining what species actually are and highlight the role of reproductive isolation. In Sect. 3, I will sketch the speciation process in the absence of gene flow and discuss why this mode of speciation is considered to be common. In Sect. 4, I present a classification of speciation scenarios based on the magnitude of gene flow, and in the following section I will discuss factors that render speciation in the presence of gene flow more complex. In the final section before the conclusions, I review a recent model that suggests that speciation in the presence of gene flow might be more common than previously thought.

The Biological Species Concept and Reproductive Isolation

Thinking about the process of speciation requires a species definition. To a large extent the biological diversity surrounding us is not continuous but rather falls into more or less discrete clusters. Everybody can distinguish a frog from a bird, a duck from a finch and a chaffinch from a house sparrow. Based on a system introduced by the Swedish botanist Carl von Linné, biologists classify organisms into a nested hierarchy with species being the basal unit. Similar (and therefore related) species are grouped into genera, similar genera into families, families into orders, orders into classes and classes into kingdoms. However, delineating species from each other has proven more difficult than one might think. On the one hand, many organisms that one would naively assign to different species because of their differing appearance can interbreed, and their intermediate offspring blur the boundaries between species. On the other hand, in many cases, subtle differences occur between individuals within a species, such that some taxonomists prefer to split the species into two distinct species while others consider the differences too minor for such a split.

The reason for these difficulties is that the evolutionary process leading to speciation is inherently continuous. The split of one species into two daughter species does generally not occur in a single step but through the accumulation of many changes of small effect. Thus, depending on the stage of a particular speciation event, a clear distinction is either possible or not. To cope with these difficulties, many different species concepts have been developed (for a review, see Coyne and Orr, 2004).

For sexually reproducing organisms, the most popular of these concepts was suggested by Ernst Mayr (1942). According to his *biological species concept*, a species is a group of potentially interbreeding organisms. Thus, by definition, different species have to be *reproductively isolated* from each other. For the following discussion, it will be useful to distinguish two types of *reproductive barriers*:

- *Prezygotic barriers* prevent the union of a female egg and a male sperm and therefore the formation of a *zygote* (a fertilized egg). Prezygotic barriers include habitat differences that prevent potential mating partners from encountering each other, mismatches between male sexual signals and female sexual preferences, mechanical mismatches between male and female sexual organs and biochemical mismatches between sperm and egg.
- *Postzygotic barriers* act after a zygote has been formed. These barriers include reduced viability of embryos and sterility or reduced fertility of hybrids (as is the case in the hybrids between horse and donkey).

Thus, according to the biological species concept, the problem of speciation comes down to the question of how reproductive barriers — be they prezygotic or postzygotic

— evolve in a population that originally lacks any such barriers. The simplest and most widely accepted scenario is based on a spatial subdivision of a population into two or more isolated subpopulations.

Speciation in the Absence of Gene Flow

The origin of new species from geographically isolated subpopulations is called *allopatric speciation*. In this scenario, an originally connected population becomes separated into two (or more) distinct subpopulations. This separation can either be due to a geological event such as the rise of a mountain range or the spread of glaciers in an ice age, or because a few individuals colonize a new geographic region such as a remote island.

How do different species evolve in spatial isolation? Several well-established routes towards reproductive isolation in allopatry have been described (Coyne and Orr 2004). One possibility is that isolated subpopulations evolve different sexual mating signals such as body coloration or vocalization. Then, if individuals from subpopulations that have diverged in sexual signals encounter each other, they might not recognize each other as conspecifics anymore. For instance, consider a bird population with a red plumage that becomes separated into two isolated subpopulations. Now let us consider a *mutation* (a random change in the genetic code of an individual) that changes plumage colour to blue with no effect on fitness. Such a mutation might increase in frequency purely by chance and ultimately become fixed in the subpopulation where it had originally occurred (Figure 1a). If mate recognition is based on colour, then a prezygotic reproductive barrier has evolved between the two subpopulations.

In the previous example, the mating barrier arose by chance. Alternatively, if the environment differs between geographic regions, then the isolated subpopulations are expected to evolve different characters so as to be adapted to their local environment, and mating barriers can emerge as a by-product of local adaptation. For instance, plumage colours can diverge in response to differences in the local environment such that plumage colour itself is a local adaptation.

The next scenario involves local adaptation to different food resources, an idea that will reoccur throughout this chapter. Assume that in one geographic region, plants producing small seeds are predominant while in another region, plants producing large seeds are predominant. If these two regions are inhabited by a seed-eating bird species, the expectation is that the subpopulation inhabiting the region with small seeds evolves a small bill, suitable for feeding on small seeds, while the subpopulation inhabiting the other region evolves a large bill, suitable for feeding on large seeds (Figure 1a). If, for some reason, birds preferentially mate with partners having a similar-sized bill, such that small-billed birds mate with small-billed birds and large-billed birds mate with large-billed birds, a prezygotic mating barrier has evolved as a by-product of local adaptation to different food resources. A specific reason why this might be the case is that bill morphology also affects song production (Podos 2001) and mate choice in birds is often influenced by song. Thus, as a side effect of their bill size, small-billed birds sing differently than large-billed birds and therefore attract different partners.

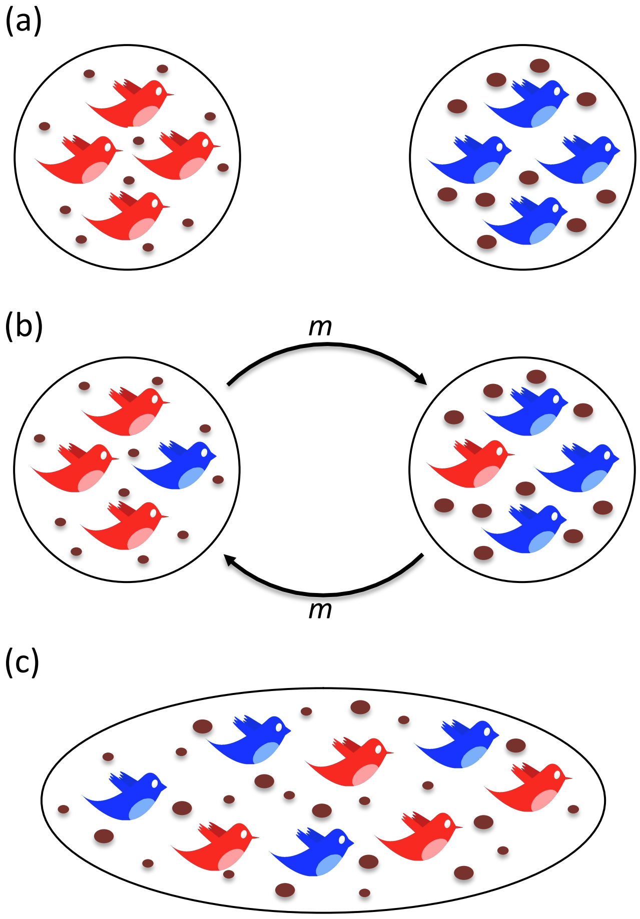

Fig. 1 Classification of geographic modes of speciation. **(a)** Speciation is allopatric when it occurs in two spatially isolated subpopulations. **(b)** Speciation is parapatric when it occurs in a spatially subdivided population with limited gene flow. Here m is the proportion of individuals exchanged between the two subpopulations per generation. **(c)** Speciation is sympatric when it occurs within a single undivided population. Note that for m=0, the parapatric scenario is equal to the allopatric scenario while for m=1/2, the parapatric scenario is equal to the sympatric scenario. In **(a)** and **(b)** the two geographic regions differ in the spectrum of available seeds (small or large). Red birds have a small bill, suitable to forage on small seeds, while blue birds have a large bill, suitable for large seeds.

In the previous examples, mating barriers were prezygotic. Another scenario believed to be common is the evolution of postzygotic barriers by so-called *Dobzhansky-Muller incompatibilities* (Coyne and Orr 2004, Presgraves 2010). This theory is based on the fact that different mutations are expected to accumulate in isolated subpopulations. Importantly, mutations are selected in the genomic background where they arose. If individuals from different subpopulations mate with each other, mutations in different genes that arose in different genomic backgrounds become combined in one genome in their offspring. Such new gene combinations often show negative interactions in their effect on fitness, such as reduced viability and fertility, causing postzygotic isolation.

The important point in the allopatric scenario is that reproductive isolation is expected to evolve almost inevitably if the time separating the subpopulations is long enough (Coyne and Orr 2004). Therefore, this route to speciation is also referred to as *by-product speciation*.

Speciation in the Presence of Gene Flow

Although many evolutionary biologists believe that the vast majority of speciation events have occurred in allopatry, this view has been challenged repeatedly and fervently. Darwin himself made some statements in “The Origin of Species”, which seem to argue in favour of speciation in the absence of spatial barriers. Before we delve deeper into the role of gene flow for speciation, I will finish the classification of speciation in terms of the geographical setting that I started by introducing allopatric speciation.

Consider a system of two subpopulations that exchange a proportion $m \leq 1/2$ of their members each generation (Figure 1b). Thus, m describes the magnitude of migration between the two subpopulations. Assume that mating follows migration and is random within each subpopulation. If $m=0$, then the two subpopulations coexist in allopatry (Figure 1a). If $m=1/2$, then individuals will live with equal probability in each of the two subpopulations: They are randomly distributed. This scenario is in fact equivalent to the absence of any spatial subdivision (Figure 1c). Speciation in such a setting is called *sympatric speciation*. If $0<m<1/2$, then individuals are more likely to live in the subpopulation where they were born (Figure 1b). With decreasing strength of migration, the population becomes increasingly subdivided. If speciation occurs in this setting, it is called *parapatric speciation*. Thus, the three modes of speciation are part of a continuum.

Sympatric Speciation

Sympatric speciation can be viewed as the opposite of allopatric speciation. It occurs when new species arise from within a single interbreeding population (Figure 1c). More precisely, Gavrilets (2004) defines sympatric speciation as “the emergence of new species from a population where mating is random with respect to the birthplace of the mating partner”. For the longest time, sympatric speciation was considered very unlikely due to the lack of convincing empirical examples and theoretical difficulties.

However, in the last 20 years, new theoretical results and empirical findings have increased the credibility of this idea (e.g. Dieckmann et al. 2004a). It is now widely accepted that sympatric speciation is in principle possible, but what remains disputed is its importance in nature. While some researchers believe that it is likely to be rare (e.g. Coyne and Orr 2004, Gavrilets 2003, 2004), others are far less restrictive in their view (e.g. Dieckmann et al. 2004a, Doebeli et al. 2005).

Since allopatric speciation is considered easy, the burden of proof lies on sympatric speciation. This proof is inherently difficult since it requires evidence that two species never experienced an allopatric phase in their evolutionary history (Coyne and Orr 2004). Not surprisingly, well-established examples come from species pairs occupying small and isolated habitats where it is difficult to envisage a spatial subdivision (for a review, see Bolnick and Fitzpatrick 2007). Such examples include palm trees on oceanic islands (Savolainen et al. 2006) and cichlid fish in volcanic crater lakes (Barluenga et al. 2006).

Parapatric Speciation

Parapatric speciation occurs in spatially subdivided populations with gene flow between the different subpopulations (Figure 1b). The fact that allopatric and sympatric speciation are extremes where mixing is either absent or complete, respectively, suggests that parapatric speciation should be the most widespread scenario. It can be viewed either as similar to allopatric speciation but more difficult because of increased gene flow or as similar to sympatric speciation but somewhat easier because of decreased gene flow. Despite the expected generality of parapatric speciation it has received less attention by theoretical evolutionary biologists than the other scenarios. Most likely this is the case because parapatric speciation is more difficult to study. In Sect. 6, I will review a recent mathematical model investigating parapatric speciation that injects new vigour into the idea of speciation with gene flow.

Obstacles to Speciation with Gene Flow

Why is speciation in the presence of migration considered more difficult than allopatric speciation? To answer this question, we have to review some requirements for speciation. Consider two bird species, one of them with a red plumage and the other with a blue one. Assume that the two species are reproductively isolated because red mates with red and blue mates with blue. If the two species are identical in all other aspects, then we know from the theory of stochastic processes that it will only be a question of time until one species goes extinct. This happens because, through the eye of natural selection, the two species are identical, and thus, purely by chance, one species will increase in frequency and ultimately replace the other one.

Now assume that individuals of the red species have a small bill while individuals of the blue species have a large bill and that small bills are more suitable for feeding on small seeds while large bills are more suitable for feeding on large seeds. Assume, furthermore, that these birds live in an environment with two habitats, one with plants producing small seeds and one with plants producing large seeds and that birds migrate between the habitats with rate *m* (Figure 1b). If the small-billed red species is rare while the large-billed blue species is common, small seeds will be abundant while large seeds will be depleted. Then individuals of the red species find plenty of food, while individuals of the blue species struggle to find food. As a consequence, red birds can raise more offspring than blue ones, letting the former increase in frequency while the latter decrease in frequency. The opposite story can be told if the situation is reversed and we start with a population where initially the large-billed blue species is rare while the small-billed red species is common. Thus, in this setting, each species can increase in frequency when rare. This results in stable coexistence of the two species. In conclusion, for two species to stably coexist they have to differ in ecologically relevant traits.

In the above story, I assumed that bill size and plumage colour co-occur in specific combinations — small-billed birds were red while large-billed birds were blue — and that mate choice is based on colour matching. With these assumptions, small-billed birds mate with small-billed birds and large-billed birds mate with large-billed birds. If this were not the case, that is, if small-billed birds would mate with large-billed birds, many of their offspring would have bills of intermediate size. As a consequence, the ecological differences would become blurred resulting in a single species with intermediate bill size. The take-home message is that speciation with gene flow requires the evolution of distinct ecological traits and a system of mate choice where individuals with similar ecological traits mate with each other (if this is the case, mating is called *assortative*). Then the ecological differences are maintained in a sexually reproducing population. In the following, I will review these requirements in more detail.

Ecological Differentiation. For a species to split into two new species it has to diverge into two ecologically differentiated types that can stably coexist. But when should a bird population characterized by medium-sized bills, allowing to feed reliably, although not splendidly, on both small and large seeds, differentiate into two subpopulations with small-billed and large-billed birds, respectively? This requires a special form of natural selection where individuals with extreme traits (e.g. large and small bills) have a higher fitness than individuals with intermediate traits. Such *disruptive selection* is a crucial ingredient of most recent models for speciation with gene flow. Importantly, this type of selection has by now been documented to occur in several natural populations (Bolnick and Fitzpatrick 2007), and an ecological setting as considered here with two alternative resources is a prime candidate.

Prezygotic Reproductive Isolation. In a population experiencing disruptive natural selection, mating between extreme phenotypes produces intermediate unfit offspring. In our example, birds with intermediate bills are expected to eat fewer seeds than small-billed and large-billed birds and therefore have reduced fitness. This is a form of postzygotic isolation due to the ecological circumstances. (It is therefore fundamentally different from the postzygotic isolation due to Dobzhansky-Muller incompatibilities discussed earlier.) As a consequence, any mechanism preventing the production of intermediate types would be favoured by selection. This is in particular true for assortative mating (a prezygotic barrier) between ecologically differentiated individuals such that small-billed birds preferentially mate with small-billed partners while large-billed birds preferentially mate with large-billed partners. How can assortative mating evolve? An easy mechanism is in place if, for some reason, all individuals have the preference: “mate with individuals that resemble yourself”. To illustrate this case, consider an insect that can lay its eggs on two different types of fruits, and it generally does this on the fruit to which it is better adapted. If mating takes place just before egg deposition, that is, on the fruit, then automatically mating occurs preferentially between individuals specialized for the same fruit. Ecological traits that have the property that mating between similar types occurs automatically are known, but their abundance is unclear (Servedio et al. 2011).

Linkage Between Ecological Trait and Mating Trait. Alternatively to the previous scenario, females can evolve a trait-specific preference. In this case, the population does diverge not only in the ecological trait but also in the female mating preference. Now consider the scenario that mating preferences diverge such that small-billed females have a preference for large-billed males and vice versa. Then speciation does not happen because the ecological differences become blurred. Hence, what is needed is an association between the ecological character (bill size) and the mating preference, such that indeed alike mates with alike. In terms of our example, the genes coding for a small bill have to occur in the same individual as the genes coding for the preference for small-billed partners, while the genes coding for a large bill have to occur in the same individual as the genes coding for a preference for large-billed partners. The situation is even more complex if the mating preference is with respect to a trait not related to the ecological trait, such as plumage colour. Then the genes coding for a small bill have to occur in the same individual as the genes coding for a red plumage *and* the genes coding for a preference to mate with red males. Although models have been proposed where just such associations do evolve (Dieckmann and Doebeli 1999), it is this obstacle that lets many evolutionary biologists be rather sceptical towards speciation in the presence of gene flow. An elementary force destroying such associations is *recombination*. Diploid organisms carry for every gene two copies, one received from the father and one from the mother. During the production of egg and sperm cells, these copies become shuffled into new combinations such that the copy of the gene for bill size received from the mother can be combined with the copy of the gene for plumage colour received from the father end up in the same egg or sperm cell, respectively.

A Realistic Route to Speciation in the Presence of Gene Flow by Sexual and Natural Selection

A preliminary conclusion from the above considerations and one that is shared by many evolutionary biologists is that speciation in the face of significant gene flow is in principle possible but very difficult and therefore likely not to be a very common. The major obstacle to speciation with gene flow, for which no general and satisfying solution has been found, is that mating preferences have to diverge and to become linked to a diverged ecological trait.

Recently, van Doorn et al. (2009) proposed a new mechanism facilitating parapatric speciation. Their starting point is based on the following two observations: First, many male traits are costly to produce, and only individuals that are in good health are able to do so. Prime examples include colourful ornaments in many bird species. Second, females, as the choosy sex, prefer to mate with males that do show such costly signals. van Doorn and co-workers suggest that this mating structure could be the key to understanding parapatric speciation. To investigate this, they studied a mathematical model. In this section, I will briefly describe the assumptions of their model and their findings without delving into the mathematical machinery used to obtain the results.

For simplicity, I will continue to phrase the ideas in terms of birds with colourful ornaments and variable bill size, although the general mechanism is by no means

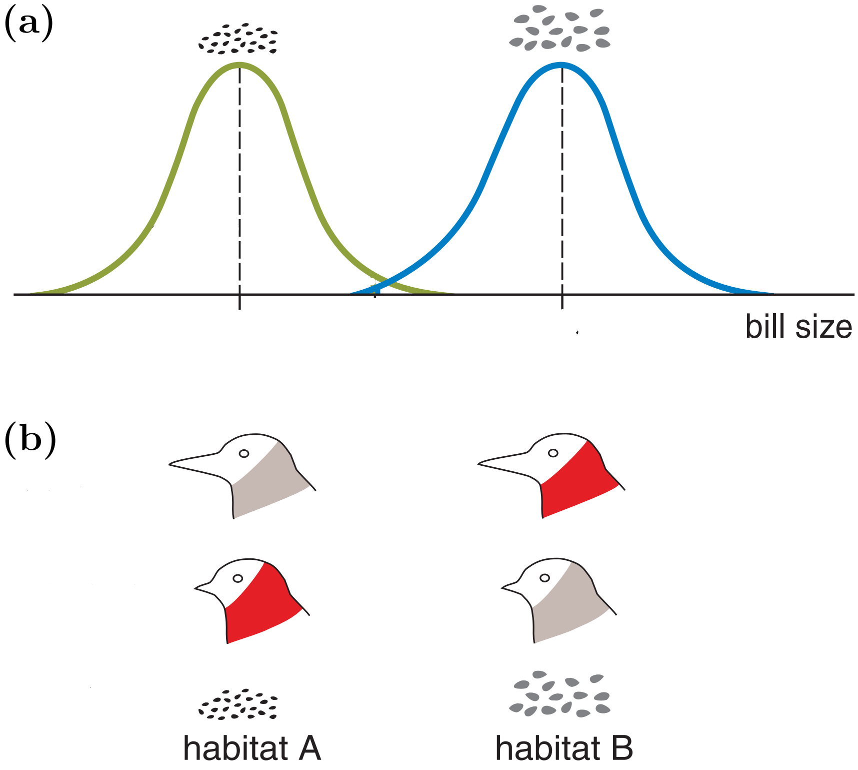

Fig. 2 Structure of the model by van Doorn et al. (2009). **(a)** The model considers an environment with two different habitats (small seeds in habitat A and large seeds in habitat B). Birds differ in an ecological character (bill size). The green Gaussian curve describes how fitness in habitat A varies with bill size x, whereas the blue curve characterizes fitness in patch B. If these curves are sufficiently narrow, selection is disruptive. **(b)** The coloured collar represents a sexual ornament that is expressed in a condition-dependent manner. For the same proportion of resources allocated to the ornament, small-billed birds can produce a more attractive (red) ornament in the small-seed habitat A, whereas large-billed birds can produce a more attractive ornament in the large-seed patch B. Hence, the ornament functions as an indicator of local adaptation. From van Doorn et al. (2009). Reprinted with permission from AAAS.

restricted to this scenario. Assume that two habitats exist, one where mainly small seeds can be found and one where mainly large seeds can be found. Assume again that birds with small bills can efficiently feed on small seeds, while birds with large bills can efficiently feed on large seeds. Young birds migrate between the two habitats with probability m and, given they survive to adulthood, mate and reproduce within their habitat. The amount of resources an individual can gather has two consequences. First, it determines the survival probability of newborns to adulthood for both males and females. Birds with a bill that matches the seed size in their habitat have a higher probability to reach maturity than birds for which bill size and seed size do not match. Second, resource

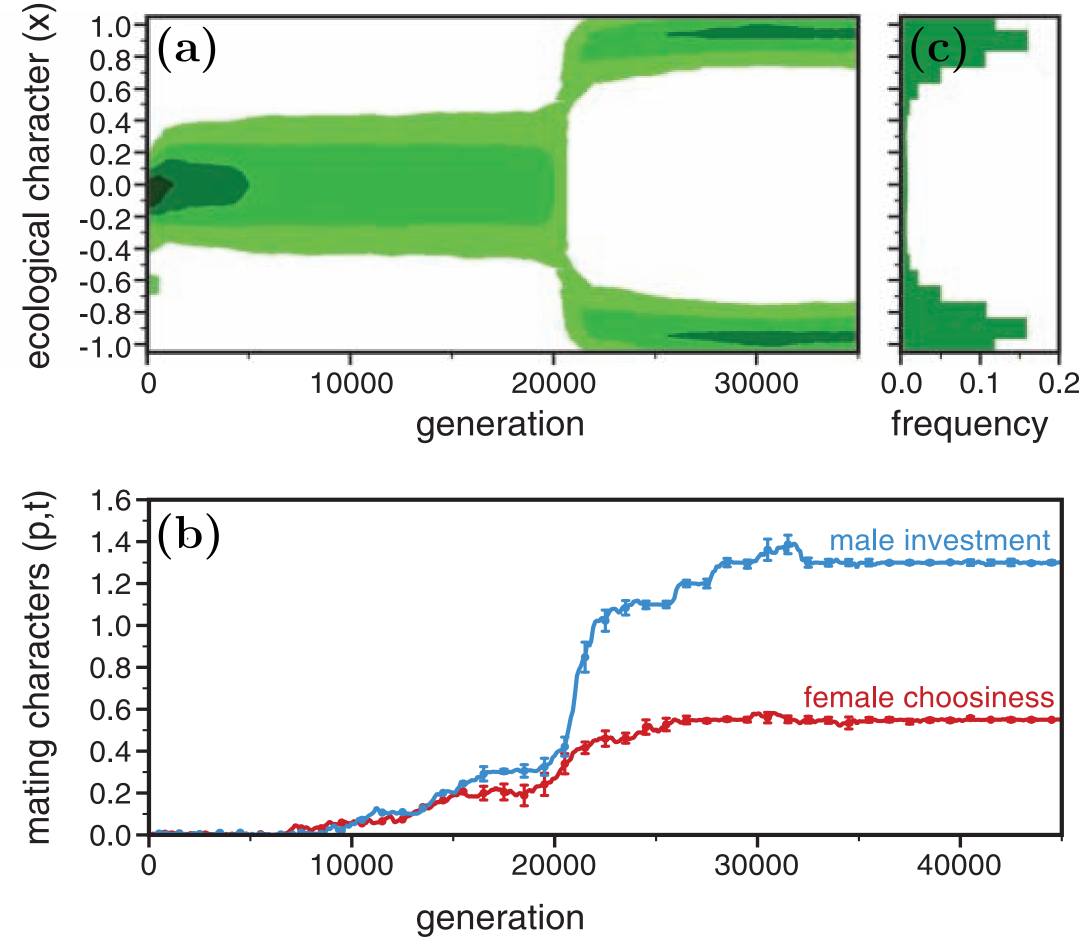

Fig. 3 Example simulation of the model by van Doorn et al. (2009). Sexual selection on a trait signaling male quality can cause reproductive isolation between two ecologically specialized populations, while natural selection alone cannot. **(a)** During the evolution of a costly female mating preference p (shown by the red line in **(b)**) for a male ornament, the population splits into two ecological specialists. The ornament reflects a costly male investment t (blue line in **(b)**) and the degree of the male's adaptation to local conditions. Error bars in **(b)** denote the standard deviation of p and t to indicate the standing genetic variation in these traits. **(c)** Distribution of the ecological trait x in the population at the end of the simulation. The near absence of any intermediate phenotypes indicates successful speciation. From van Doorn et al. (2009). Reprinted with permission from AAAS.

acquisition determines the amount of energy males can invest into the costly ornament. Males with a bill matching the seed size in their habitat have a bright plumage, while males with a bill not matching the seed size have a dull plumage (Figure 2).

In their model, van Doorn et al. assume that three different traits can evolve. The first trait is the ecological character x that determines feeding efficiency in different habitats. To stick to our example, an x-value of -1 corresponds to a small bill, optimally adapted to small seeds. Increasing x corresponds to increasingly larger bills, and an x-value of +1 corresponds to a large bill, optimally adapted to large seeds. The second trait is the proportion t of energy males invested into the costly ornament. The ornament is costly because energy that is invested into the ornament cannot be invested into survival, such that males with a high value of t have a lowered probability to reach maturity. The third trait is the choosiness p of females. It determines how much attention females actually pay during mate choice to the male ornament. Larger values of p indicate that females have a stronger preference for males with an elaborate ornament.

The predictions based on their model are summarized in Figure 3. van Doorn et al. assume that in the initial population, males do not invest into the ornament (t=0) and that females pay no attention to the ornament (p=0). In the absence of any mating barriers, the population quickly evolves a unimodal distribution around the generalist phenotype x=0 (Figure 3a, up until generation 20000). The reason is that, due to migration and recombination, the genes of specialized phenotypes become mixed, leading to a more or less Gaussian distribution around the least adapted phenotype (x=0). As noted above, disruptive selection is an essential ingredient for speciation in the face of gene flow, and van Doorn et al. focus on this scenario. Under this condition, any mechanism that prevents the production of unfit intermediate phenotypes is selectively favoured. In each of the two habitats, locally adapted individuals are more likely to survive until sexual maturity. Thus, by preferring brightly coloured males, females are likely to mate with males that are adapted to the same environment as she herself. As a consequence, such females are likely to produce more locally adapted offspring, which gives females with higher p-values a selective advantage. Once females have evolved such a preference, males are selected to invest more into their ornament so as to father more offspring (this type of selection for mating success is also called *sexual selection*). Initially, both the preference and the intensity of the plumage coloration increase slowly (Figure 3b, up until generation 20000). Meanwhile, birds with small and large bills become more frequent while birds with intermediate bills become more rare, until, finally, the distribution of bill sizes becomes bimodal (Figure 3c). This, in turn, strengthens selection for assortative mating resulting in a further increase of female preference and male investment (Figure 3a and b, from generation 20000 onwards). This feedback between natural and sexual selection finally results in two different species that do not interbreed anymore.

The important finding of van Doorn et al. is that, with sexual selection on a condition-dependent male ornament, speciation can occur without divergence in female mating preferences and despite high migration rates by which the emergence of new species would otherwise be prevented.

Conclusions

The dominant view among evolutionary biologists is that most speciation events took place in allopatry, that is, in spatially isolated subpopulations. However, in the last 20 years, the idea that speciation can take place in the presence of considerable gene flow has gained more credibility. This is due to new mathematical models that solved some problems previously thought insurmountable and to new empirical examples with strong evidence for speciation in either sympatry or parapatry. Thus, the focus of the debate has shifted from the question whether speciation in the presence of gene flow can occur at all towards how frequent this mode of speciation really is.

This changing attitude is accompanied by a shift in emphasis from the spatial pattern towards the processes underlying speciation. In other words, the focus in speciation research has moved from the geographical context towards an understanding of the relative roles of selection, gene frequency changes through chance events (*drift*) and external chance events such as the formation of geographic barriers (Dieckmann et al. 2004b, van Doorn 2004, Weissing et al. 2011).

Ultimately, the role of gene flow in speciation is an empirical question, and ideally, our view should be determined by data. Modern molecular techniques are likely to give us a more precise picture of the role of gene flow in speciation in the near future. However, due to the historical nature of the speciation process, definite answers will often not be possible. This is especially true for speciation events that are only documented in the fossil record. Thus, understanding the role of migration in speciation is likely to stay an active research area for a long time to come.

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