

17. Alley, R. B., Blankenship, D. D., Rooney, S. T. & Bentley, C. R. Sedimentation beneath ice shelves—the view from Ice Stream B. *Mar. Geol.* **85**, 101–120 (1989).

18. Aksu, A. E. & Hiscott, R. N. Shingled Quaternary debris flow lenses on the north-east Newfoundland slope. *Sedimentology* **39**, 193–206 (1992).

19. Hiscott, R. N. & Aksu, A. E. Submarine debris flows and continental slope evolution in front of Quaternary ice sheets, Baffin Bay, Canadian Arctic. *Am. Assoc. Petrol. Geol. Bull.* **78**, 445–460 (1994).

20. Hesse, R., Klauke, L., Ryan, W. B. F. & Piper, D. J. W. Ice-sheet sourced juxtaposed turbidite systems in the Labrador Sea. *Geosci. Can.* **24**, 3–14 (1997).

21. Dowdeswell, J. A. & Siegert, M. J. Ice-sheet numerical modeling and marine geophysical measurements of glacier-derived sedimentation on the Eurasian Arctic continental margins. *Geol. Soc. Am. Bull.* **111**, 1080–1097 (1999).

22. Elverhøi, A. *et al.* The growth and decay of the Late Weichselian ice sheet in western Svalbard and adjacent areas based on provenance studies of marine sediments. *Quat. Res.* **44**, 303–316 (1995).

23. Fisher, D. A., Reeh, N. & Langley, K. Objective reconstruction of the Late Wisconsinan Laurentide Ice Sheet and the significance of deformable beds. *Geogr. Phys. Quat.* **39**, 229–238 (1985).

24. Hesse, R. *et al.* Imaging Laurentide Ice Sheet drainage into the deep sea: impact on sediments and bottom water. *GSA Today* **6**, 3–9 (1996).

25. Hesse, R. & Khadabakhsh, S. Depositional facies of late Pleistocene Heinrich events in the Labrador Sea. *Geology* **26**, 103–106 (1998).

26. Dowdeswell, J. A. & Murray, T. in *Glacimarine Environments: Processes and Sediments* (eds Dowdeswell, J. A. & Scourse, J. D.) 121–137 (Spec. Publ. 53, Geological Soc., London, 1990).

27. Johannesson, T., Raymond, C. & Waddington, E. Time-scale for adjustment of glaciers to changes in mass balance. *J. Glaciol.* **35**, 355–369 (1989).

28. Dansgaard, W. *et al.* Evidence for general instability of past climate from a 250-kyr ice-core record. *Nature* **364**, 218–220 (1993).

29. Baumann, K.-H., Lackschewitz, K. S., Erlenkeuser, H., Henrich, R. & Jünger, B. Late Quaternary calcium carbonate sedimentation and terrigenous input along the East Greenland continental margin. *Mar. Geol.* **114**, 13–36 (1993).

30. Dokken, T. & Hald, M. Rapid climatic shifts during isotope stages 2–4 in the Polar North Atlantic. *Geology* **24**, 599–602 (1996).

31. Hebbeln, D. & Wefer, G. Late Quaternary paleoceanography in the Fram Strait. *Paleoceanography* **12**, 65–78 (1997).

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## Interactions among quantitative traits in the course of sympatric speciation

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Sympatric speciation, the origin of two or more species from a single local population, has almost certainly been involved in formation of several species flocks<sup>1–4</sup>, and may be fairly common in nature<sup>5</sup>. The most straightforward scenario for sympatric speciation requires disruptive selection favouring two substantially different phenotypes, and consists of the evolution of reproductive isolation between them followed by the elimination of all intermediate phenotypes<sup>6</sup>. Here we use the hypergeometric phenotypic model<sup>7–10</sup> to show that sympatric speciation is possible even when fitness and mate choice depend on different quantitative traits, so that speciation must involve formation of covariance between these traits. The increase in the number of variable loci affecting fitness facilitates sympatric speciation, whereas the increase in the number of variable loci affecting mate choice has the opposite effect. These predictions may enable more cases of sympatric speciation to be identified.

According to Darwin, competition for diverse resources can lead to disruptive selection and, eventually, to sympatric speciation. “... the more diversified the descendants from any one species become ..., by so much will they be better enabled to seize on many and widely diversified places in the policy of nature, and so be enabled to increase in numbers. ... the competition will generally be most severe between those forms which are most nearly related to each other in habits, constitution, and structure. Hence all the intermediate forms ..., as well as the original parent-species itself,

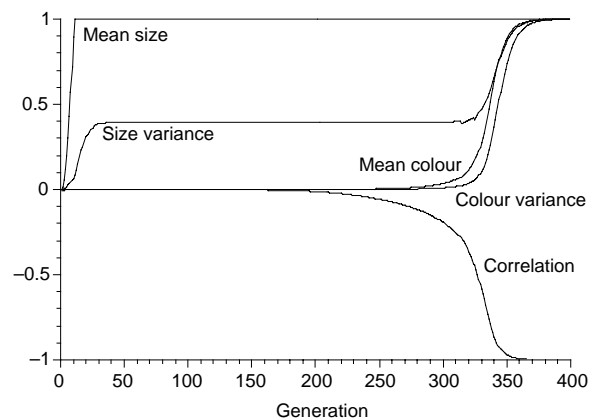
will generally tend to become extinct” (ref. 11, pp. 112, 121).

Even closely related species usually differ from each other at least at several loci<sup>5</sup>. Thus, multilocus models of sympatric speciation must be studied because single-locus models have very peculiar properties<sup>6,12</sup>. When a polygenic, quantitative trait is under disruptive selection, indirect selection favours reproductive isolation between the opposite, extreme phenotypes<sup>7,9,13–15</sup>. If such isolation evolves as a result of fixation of alleles that cause assortative mating based on this trait<sup>16,17</sup>, the same variable quantitative trait will determine both fitness and mate choice of an individual. Then, according to the data from numerical analysis<sup>9,10</sup> and individual-based computer simulations<sup>15,18</sup>, extinction of intermediate phenotypes and sympatric speciation are possible.

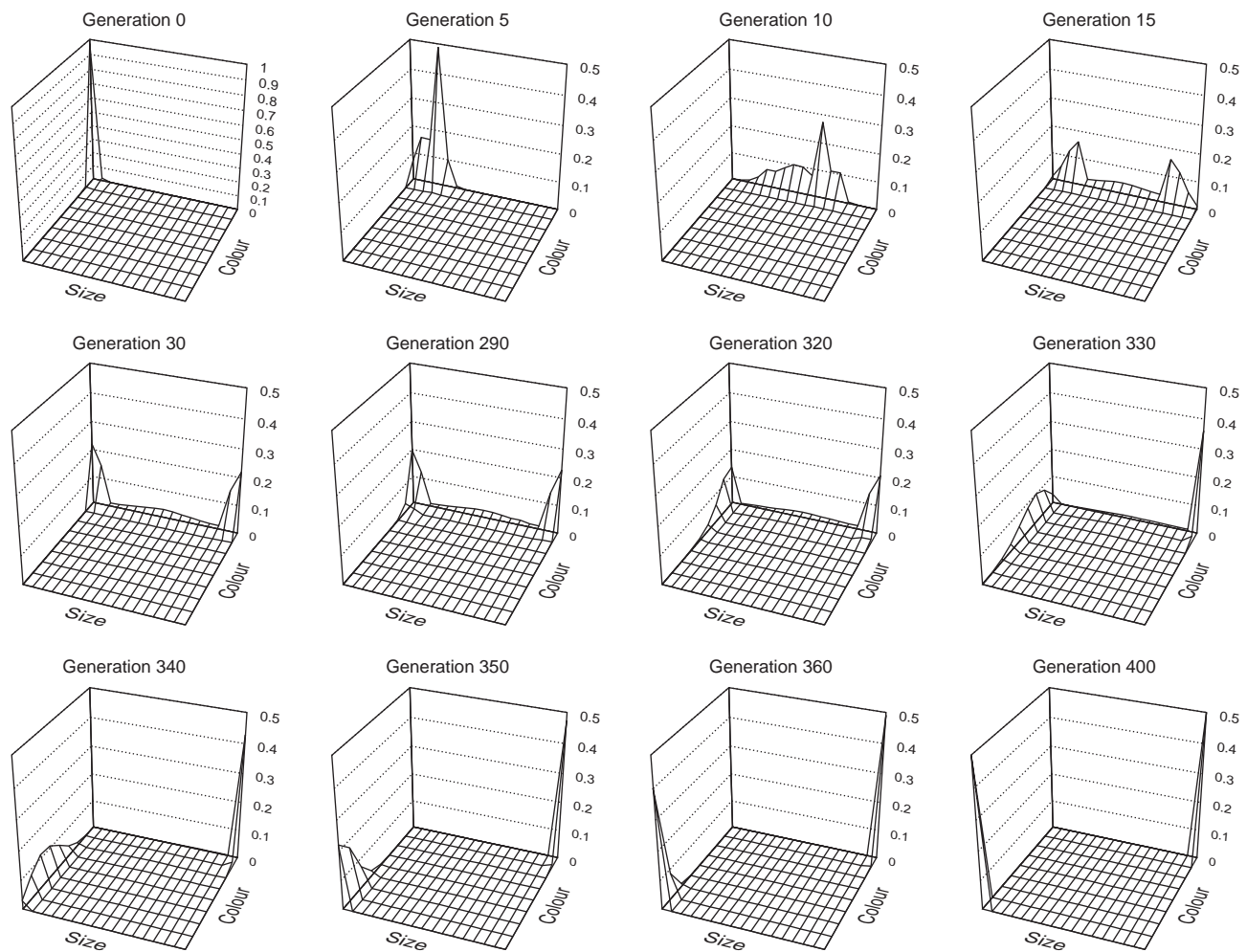
Here we study a more complex and perhaps a more realistic case where fitness and mate choice depend on different quantitative traits. We assume that variability in each trait is caused by its own set of independently transmitted loci so that speciation must involve the establishment of a linkage disequilibrium between polymorphic loci controlling fitness and mate choice. This presents an extra obstacle to speciation<sup>16,17,19</sup>, although some individual-based simulations<sup>15</sup> have suggested that it may still be possible.

In the first model, disruptive selection depends on trait 1 (size) and mate choice depends on trait 2 (colour). Colour is manifested in both females and males and the ability of two individuals to mate depends on the difference between their colours. A typical case of sympatric speciation in a population that was initially almost monomorphic in both traits is presented in Figs 1 and 2. First, frequency-dependent selection, caused by availability of two distinct resources<sup>9,18</sup>, rapidly establishes polymorphism in size such that individuals with intermediate sizes have low frequencies because they lose out in competition for either resource. Then, disruptive selection slowly increases the magnitude of the covariance between size and colour, owing to the increasing linkage disequilibria between the corresponding loci. Variability of colour also increases slowly, being driven by indirect selection resulting from this covariance. When colour becomes significantly variable, the intertrait covariance increases rapidly and individuals of intermediate sizes and colours disappear rapidly, completing sympatric speciation in the course of relatively few generations. As in the single-locus case<sup>16</sup>, the phenotypes of the two new species depend on the sign of the initial intertrait covariance. Thus, these species may consist either of ‘small red’ and ‘large blue’ or of ‘small blue’ and ‘large red’ individuals.

We can think of this process as the recruitment of colour for providing reproductive isolation between the individuals of the



**Figure 1** The dynamics of means and variances of size and colour and of the intertrait correlation in the course of sympatric speciation with two traits. The means and variances of size and colour are shown as ratios over their values corresponding to the coexistence of two equally frequent species. Variability of size depends on 16 loci and variability of colour depends on 8 loci. The relative fitness of individuals with intermediate size is 0.15.



**Figure 2** The dynamics of phenotype frequencies in the course of sympatric speciation in the same run as in Fig. 1.

opposite size. A population with zero intertrait covariance can be at equilibrium, but this equilibrium may be locally unstable. If so, recruitment can begin from the increase of even a small variance created by random drift or other factors<sup>16</sup>. Similarly, an equilibrium with zero linkage disequilibrium can be unstable in the two-locus selection–recombination model under symmetric selection<sup>20</sup>.

Table 1 shows the minimal depths of the fitness valley, defined as the ratio of the fitness of individuals with intermediate sizes over that of individuals with extreme sizes, which is necessary for the increase of the initially small covariance and eventual sympatric speciation. When differences at just two haploid loci are enough for reproductive isolation, speciation occurs as a result of assortative mating alone, even without selection<sup>12</sup>. When variability of size is due to only two loci, extreme genotypes are frequent even in a panmictic population and speciation does not happen. Generally, the increase in the number of loci affecting size facilitates speciation, and the increase in the number of loci affecting colour has the opposite effect.

In the second model, disruptive selection depends on trait 1 (size), female mate choice depends on trait 2 (preference), and male attractiveness to females depends on trait 3 (colour). The willingness of a female to mate a male depends on the difference between their preference and colour. A typical course of speciation is presented in Fig. 3. The first stage of the process, the establishment of polymorphism in size, is the same as in the first model. In addition, the small positive covariance between preference and colour develops rapidly, owing to assortative mating. Size–preference and size–colour covariances then increase slowly, causing a

slow increase in the variabilities of preference and colour. Eventually, these processes accelerate and all intermediate individuals disappear rapidly. The resulting pair of new species may consist either of ‘small, red-preferring red’ and ‘large, blue-preferring blue’ or of ‘small, blue-preferring blue’ and ‘large, red-preferring red’ individuals, depending on the signs of initial size–preference and size–colour covariances. Table 2 shows the minimal depths of the fitness valley required for the growth of initially small covariances and eventual speciation. If variability in both preference and colour is due to just one haploid locus, no selection is necessary for speciation<sup>12</sup>.

Thus, sympatric speciation resulting from disruptive selection and assortative mating is possible even when variability of fitness and mate choice depend on different, independently inherited quantitative traits, provided that disruptive selection is strong and individuals with even similar genotypes make substantially different mate choices. This conclusion is consistent with the results of individual-based computer simulations (ref. 15, and A.S.K. and F.A.K., unpublished results). Naturally, the conditions required for speciation in this case are more stringent than when the same trait determines variability of fitness and mate choice<sup>15,18</sup>. However, neither catastrophic selection nor complete reproductive isolation resulting from differences at one or two loci are required.

Instead, disruptive selection that is capable of at least doubling the variance in the fitness trait is usually necessary. Even with random mating, such selection establishes bimodal distribution of phenotypes and limits genetic exchange between the opposite extreme phenotypes, owing to low fitness of the offspring from their

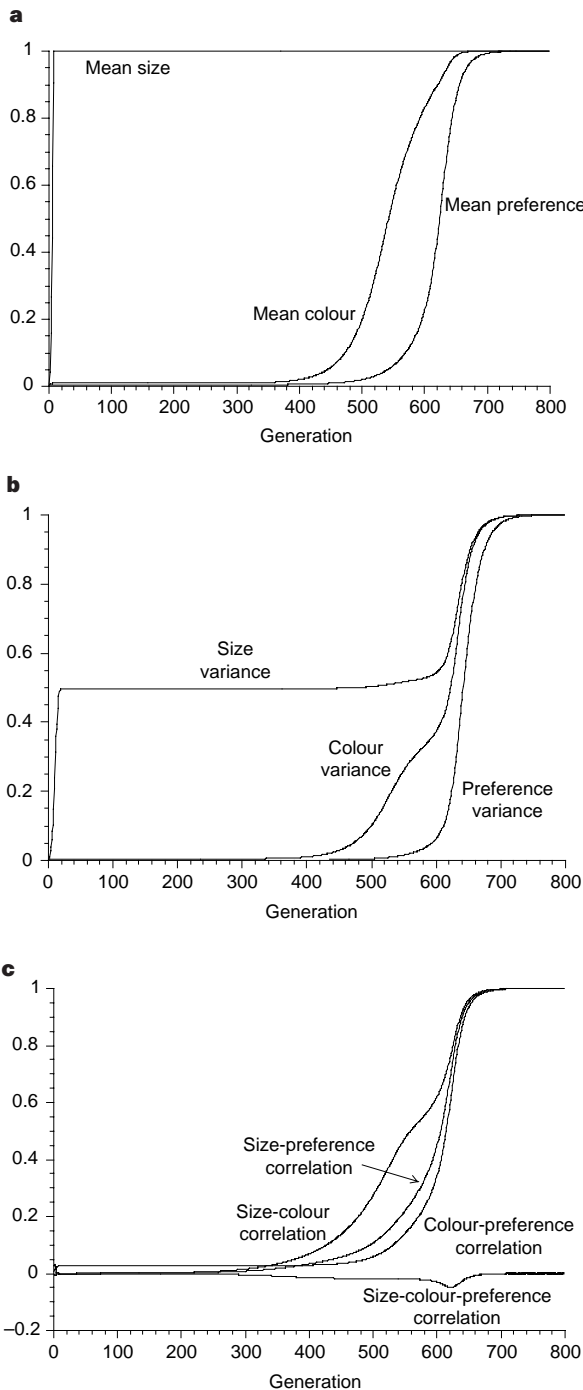
**Table 1 Maximal relative fitness of intermediate phenotypes that still lead to sympatric speciation in the two-trait model**

Number of loci	Colour 2	4	8	16	32
2	1.00	Never	Never	Never	Never
4	1.00	0.302	Never	Never	Never
8	1.00	0.377	0.178	0.094	0.033
16	1.00	0.398	0.194	0.169	0.149
32	1.00	0.416	0.194	0.170	0.158

**Table 2 Maximal relative fitness of intermediate phenotypes that still lead to sympatric speciation in the three-trait model\***

Number of loci	Male colour				
	1	2	4	8	16
1	2, 1.00	2, never	2, never	2, never	2, never
	4, 1.00	4, 0.45	4, 0.02	4, never	4, never
	8, 1.00	8, 0.42	8, 0.24	8, 0.16	8, 0.10
	16, 1.00	16, 0.43	16, 0.23	16, 0.19	16, 0.17
2	2, never	2, never	2, never	2, never	2, never
	4, 0.13	4, never	4, never	4, never	4, never
	8, 0.24	8, 0.23	8, 0.23	8, 0.23	8, 0.23
	16, 0.25	16, 0.23	16, 0.23	16, 0.23	16, 0.23
4	2, never	2, never	2, never	2, never	2, never
	4, never	4, never	4, never	4, never	4, never
	8, 0.18	8, 0.16	8, 0.16	8, 0.16	8, 0.15
8	8, 0.10	8, 0.10	8, 0.10	8, 0.10	8, 0.08
	16, 0.19	16, 0.19	16, 0.19	16, 0.19	16, 0.19
16	2, never	2, never	2, never	2, never	2, never
	4, never	4, never	4, never	4, never	4, never
	8, 0.04	8, 0.04	8, 0.04	8, 0.04	8, 0.04
	16, 0.15	16, 0.15	16, 0.15	16, 0.15	16, 0.15

\* The numbers of loci affecting trait 1 are shown within cells. Only the upper triangular part of the table is shown, because the data are symmetric.



**Figure 3** The dynamics of means and variances of size, preference and colour and of the intertrait correlations in the course of sympatric speciation with three traits. **a**, Means; **b**, variances; **c**, intertrait correlations. The means and variances of size, preference and colour are shown as ratios over their values corresponding to the coexistence of two equally frequent species. Variabilities of size, preference and colour depend on 8, 8 and 4 loci, respectively. The relative fitness of individuals with intermediate size is 0.12.

interbreeding<sup>10,18</sup>. After this, opposite phenotypes may become associated with different values of mate-choice traits, which can lead to the replacement of isolation by selection with true reproductive isolation. Genetic load may stay below 60–70% during the whole course of speciation.

Several scenarios of sympatric speciation attributed to sexual selection<sup>21–23</sup>, inspired by the apparently sympatric origin of species flocks of African cichlid fish, have been proposed recently. Although the role of sexual selection in the origin of these flocks cannot be ruled out at present, our scenario is more economical and explains all of the data. Although non-random mating due to preference-colour-trait systems<sup>24–26</sup> currently prevents interbreeding between sympatric species and must have been involved in their origin, such mating does not necessarily lead to sexual selection (that is, to differential reproductive success of different genotypes)<sup>27</sup>. Assortative mating—that is, non-random mating such that all individuals are equally successful in finding mates<sup>27</sup>—may be enough. Sympatric species of cichlids often possess different jaw morphology and have very dissimilar diets, using non-overlapping resources<sup>24</sup>. This suggests that natural as opposed to sexual selection was probably involved in their formation. In addition, because two sympatric species cannot coexist in the same ecological niche, a pair of species that seemed to evolve exclusively as a result of sexual selection would be unstable<sup>18</sup>. Indirect selection on mate-choice traits is typically only one order of magnitude weaker than the primary disruptive selection. Thus, variability in mate-choice traits may evolve despite some disadvantage of rare phenotypes as a result of sexual selection.

A pair of sympatric species that have evolved recently according to the scenario described above must have the following properties. First, the two species must be profoundly similar, with interspecific genetic differences confined to loci directly affecting the traits under disruptive selection and responsible for mate choice. Second, interspecific differences in utilization of resources must result from at least several loci. Third, reproductive isolation must be due to differences in not too many loci. Therefore, genetic analysis of morphological, ecological and behavioural differences between sympatric species of a very recent origin<sup>1–4</sup> can be used to test this scenario. □

**Methods**

**Hypergeometric model.** If the new species differ from each other at many loci, the number of possible genotypes in the speciating population is too high for the genotype-level analysis, whereas the standard phenotypic approach based on the gaussian approximation clearly cannot describe the splitting of a

population into two. Fortunately, the hypergeometric phenotypic model<sup>7–9</sup> is applicable under the conditions required for sympatric speciation<sup>10</sup>. For a quantitative trait with the possible phenotypes 0, 1, ...,  $n$ , this model provides, as a sum of certain hypergeometric functions, the probability  $R(i, j, k)$  of two parents with phenotypes  $i$  and  $j$  producing an offspring with phenotype  $k$  (refs 8–10).

**Implementation of the model.** We considered haploid individuals with the phenotype in their  $m$ -th trait determined by the number of alleles 1 at the  $n_m$  corresponding loci, each with alleles 0 and 1. The dynamics with  $n_m/2$  diploid loci are very similar<sup>10</sup>. The generations were discrete and the life cycle consisted of selection, mating and reproduction.

In the two-trait model, the frequency of  $(i_1, i_2)$  individuals of the  $i_1$ -th phenotype in trait 1 and  $i_2$ -th phenotype in trait 2 before selection was  $p(i_1, i_2)$ . After selection, this frequency become  $p'(i_1, i_2) = w(i_1)p(i_1, i_2)/W$ , where  $w(i_1)$  is the fitness function and  $W$  is the mean fitness. An individual mated no more than once. Individuals paired randomly and mating of a pair occurred with the probability  $M(d)$ , where  $d$  is the ratio of the difference between their phenotypes in trait 2 expressed as a proportion of  $n_2$ . All unmated individuals paired again, and the process continued until less than  $10^{-10}$  of the population remained unmated. In this way,  $A(i_1, i_2, j_1, j_2)$ , that is, the frequency of mating between  $(i_1, i_2)$  and  $(j_1, j_2)$  individuals, was calculated. During reproduction a pair of such parents produced an offspring  $(k_1, k_2)$  with the probability  $R(i_1, j_1, k_1)R(i_2, j_2, k_2)$ , where  $R_m$  describes the transmission of phenotypes in the  $m$ -th trait.

The three-trait model was analogous, but  $M$  depended on  $d = |i_2/n_2 - j_2/n_2|$ , where  $i_2$  and  $j_2$  were phenotypes of the first (female) and second (male) potential partners in traits 2 and 3, respectively. THINK C programs are available on request.

**Parameters.** During selection, 10% of individuals with the highest and lowest values of their phenotypes in trait 1 had fitness 1.0, and the fitness of the rest was  $D < 1.0$ . Such selection causes sympatric speciation most efficiently<sup>18</sup>.

In both models,  $M(d) = 1 - d$ , that is, the degree of reproductive isolation, grew linearly with the difference between the potential mates, but only the individuals that were maximally different were completely isolated. If such individuals were isolated but all others mated freely, speciation never occurred.

In most runs, the initial population consisted of 99.99% of individuals with phenotype 0 in all two or three traits. The rest of the population had phenotypes no more than 1 in every trait and the covariances between the traits were very small.

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- Mina, M. V., Mironovsky, A. N. & Dgebuadze, Y. Y. Lake Tana large barbs: phenetics, growth and diversification. *J. Fish Biol.* **48**, 383–404 (1996).
- Berberi, P. & Valiushok, D. Genetic divergence among morphotypes of Lake Tana (Ethiopia) barbs. *Biol. J. Linn. Soc.* **64**, 369–384 (1998).
- Schlieven, U. K., Tautz, D. & Paabo, S. Sympatric speciation suggested by monophyly of crater lake cichlids. *Nature* **368**, 629–632 (1994).
- Johnson, T. C. *et al.* Late pleistocene desiccation of Lake Victoria and rapid evolution of cichlid fishes. *Science* **273**, 1091–1093 (1996).
- Ritchie, M. G. & Phillips, S. D. F. in *Endless Forms: Species and Speciation* (eds Howard, D. J. & Berlocher, S. H.) 291–308 (Oxford Univ. Press, New York, 1998).
- Kondrashov, A. S. & Mina, M. V. Sympatric speciation: when is it possible? *Biol. J. Linn. Soc.* **27**, 201–223 (1986).
- Kondrashov, A. S. On the intensity of selection for reproductive isolation at the beginnings of sympatric speciation. *Genetika* **20**, 408–415 (1984).
- Barton, N. H. On the spread of new gene combinations in the third phase of Wright's shifting-balance. *Evolution* **46**, 551–557 (1992).
- Doebeli, M. A quantitative genetic competition model for sympatric speciation. *J. Evol. Biol.* **9**, 893–909 (1996).
- Shpak, M. & Kondrashov, A. S. Applicability of the hypergeometric phenotypic model to haploid and diploid populations. *Evolution* **53**, 600–604 (1999).
- Darwin, C. *The Origin of Species by Means of Natural Selection* (Murray, London, 1859).
- Kondrashov, A. S. & Shpak, M. On the origin of species by means of assortative mating. *Proc. R. Soc. Lond. B* **265**, 2273–2278 (1998).
- Wallace, A. R. *Darwinism*. (Macmillan, London, 1889).
- Rice, W. R. Disruptive selection of habitat preference and the evolution of reproductive isolation: a simulation study. *Evolution* **38**, 1251–1260 (1984).
- Kondrashov, A. S. Multilocus model of sympatric speciation. III. Computer simulations. *Theor. Popul. Biol.* **29**, 1–15 (1986).
- Maynard Smith, J. Sympatric speciation. *Am. Nat.* **100**, 637–650 (1966).
- Rice, W. R. & Hostert, E. E. Laboratory experiments on speciation: what have we learned in 40 years? *Evolution* **47**, 1637–1653 (1993).
- Kondrashov, A. S., Yampolsky, L. Yu. & Shabalina, S. A. in *Endless Forms: Species and Speciation* (eds Howard, D. J. & Berlocher, S. H.) 90–98 (Oxford Univ. Press, New York, 1998).
- Felsenstein, J. Skepticism towards Santa Rosalia, or why are there so few kinds of animals? *Evolution* **35**, 124–138 (1981).
- Karlin, S. General two-locus selection models: some objectives, results and interpretations. *Theor. Popul. Biol.* **7**, 364–398 (1975).

- Turner, G. F. & Burrows, M. T. A model of sympatric speciation by sexual selection. *Proc. R. Soc. Lond. B* **260**, 287–292 (1995).
- Galis, F. & Metz, J. A. J. Why are there so many cichlid species? *Trends Ecol. Evol.* **13**, 1–2 (1998).
- van Doorn, G. S., Noest, A. J. & Hogeweg, P. Sympatric speciation and extinction driven by environment dependent sexual selection. *Proc. R. Soc. Lond. B* **265**, 1915–1919 (1998).
- Axelrod, H. R. *The Most Complete Colored Lexicon of Cichlids* (TFH Publications, Neptune City, 1996).
- Seehausen, O., van Alphen, J. J. M. & Witte, F. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* **277**, 1808–1811 (1997).
- Seehausen, O. & van Alphen, J. J. M. The effect of male coloration on female mate choice in closely related Lake Victoria cichlids (*Haplochromis nyererei* complex). *Behav. Ecol. Sociobiol.* **42**, 1–8 (1998).
- Lewontin, R. C., Kirk, D. & Crow, J. F. Selective mating, assortative mating and inbreeding: definitions and implications. *Eugen. Quart.* **15**, 141–143 (1966).

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## On the origin of species by sympatric speciation

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**Understanding speciation is a fundamental biological problem. It is believed that many species originated through allopatric divergence, where new species arise from geographically isolated populations of the same ancestral species<sup>1–3</sup>. In contrast, the possibility of sympatric speciation (in which new species arise without geographical isolation) has often been dismissed, partly because of theoretical difficulties<sup>2,3</sup>. Most previous models analysing sympatric speciation concentrated on particular aspects of the problem while neglecting others<sup>4–10</sup>. Here we present a model that integrates a novel combination of different features and show that sympatric speciation is a likely outcome of competition for resources. We use multilocus genetics to describe sexual reproduction in an individual-based model, and we consider the evolution of assortative mating (where individuals mate preferentially with like individuals) depending either on an ecological character affecting resource use or on a selectively neutral marker trait. In both cases, evolution of assortative mating often leads to reproductive isolation between ecologically diverging subpopulations. When assortative mating depends on a marker trait, and is therefore not directly linked to resource competition, speciation occurs when genetic drift breaks the linkage equilibrium between the marker and the ecological trait. Our theory conforms well with mounting empirical evidence for the sympatric origin of many species<sup>10–18</sup>.**

The theory of adaptive dynamics<sup>19–22</sup> is a general framework for studying phenotypic evolution driven by ecological interactions. One of the phenomena unravelled by adaptive dynamics is evolutionary branching, during which directional selection drives a monomorphic population to a phenotype where ecological interactions induce disruptive selection and a subsequent split into two coexisting phenotypic clusters (Fig. 1a). Evolutionary branching explains the dynamic emergence and perpetuity of disruptive selection and serves as a unifying concept for understanding the evolution of polymorphisms. It is found in a wide range of models of asexual populations (see refs 22 and 23 for examples). Here we show that evolutionary branching also occurs in sexual populations and thus leads to a general theory for sympatric speciation.

We start from assumptions that are likely to be satisfied in many natural populations. Individuals vary in a quantitative character  $x$  determining resource use, as for example when beak size in birds determines the size of seeds consumed. Populations consisting of individuals of a given trait value  $x$  have density-dependent logistic growth with carrying capacity  $K(x)$ . We assume that the resource