Factors influencing progress toward sympatric speciation

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Abstract

Many factors could influence progress towards sympatric speciation. Some of the potentially important ones include competition, mate choice and the degree to which alternative sympatric environments (resources) are discrete. What is not well understood is the relative importance of these different factors, as well as interactions among them. We use an individual-based numerical model to investigate the possibilities. Mate choice was modelled as the degree to which male foraging traits influence female mate choice. Competition was modelled as the degree to which individuals with different phenotypes compete for portions of the resource distribution. Discreteness of the environment was modelled as the degree of bimodality of the underlying resource distribution. We find that strong mate choice was necessary, but not sufficient, to cause sympatric speciation. In addition, sympatric speciation was most likely when the resource distribution was strongly bimodal and when competition among different phenotypes was intermediate. Even under these ideal conditions, however, sympatric speciation occurred only a fraction of the time. Sympatric speciation owing to competition on unimodal resource distributions was also possible, but much less common. In all cases, stochasticity played an important role in determining progress towards sympatric speciation, as evidenced by variation in outcomes among replicate simulations for a given set of parameter values. Overall, we conclude that the nature of competition is much less important for sympatric speciation than is the nature of mate choice and the underlying resource distribution. We argue that an increased understanding of the promoters and inhibitors of sympatric speciation is best achieved through models that simultaneously evaluate multiple potential factors.

Introduction

Speciation can occur in several different geographic modes (allopatric, parapatric or sympatric: Gavrilets, 2003, 2004) and, within each mode, can be influenced by several factors (review in Kirkpatrick & Ravigné, 2002). Some potentially important factors include natural selection resulting from divergent environments (Felsenstein, 1981; Funk, 1998; Via et al., 2000; Schluter, 2000; Nosil, 2004), intraspecific competition (Doebeli, 1996; Dieckmann & Doebeli, 1999; Bolnick, 2004b) and

mate choice (Turner & Burrows, 1995; Kondrashov & Shpak, 1998; Higashi et al., 1999; Takimoto et al., 2000; Ritchie, 2007). (By 'divergent environments', we mean some sort of bimodality in the environment, particularly the width of the resource distribution.) The case of sympatric speciation has been of particular interest because reproductive barriers must then evolve *in situ* to prevent homogenization (Fitzpatrick et al., 2008). Thus far, theoretical models of sympatric speciation have shown the potential for each of the aforementioned factors to cause diversification under at least some circumstances. No model, however, has attempted to infer the relative importance of all three factors, including the role of interactions among them. Here we use individual-based numerical simulations to explicitly

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assess the importance of various combinations of mate choice, divergent environments (unimodal or increasingly bimodal resource distributions) and intraspecific competition on sympatric speciation. We now consider each factor in more detail.

Mate choice has been considered in a number of sympatric speciation models, either with competition (e.g. Dieckmann & Doebeli, 1999; Drossel & McKane, 2000; Kirkpatrick & Ravigné, 2002) or without competition (e.g. Kirkpatrick, 1982; Higashi et al., 1999) and either with divergent environments (e.g. Gavrilets & Vose, 2005; Gavrilets et al., 2007) or without divergent environments (e.g. Dieckmann & Doebeli, 1999; Drossel & McKane, 2000). The main finding of this body of work is that mate choice can be an important (and perhaps necessary) contributor to sympatric speciation in the presence of disruptive natural selection owing to divergent environments and/or intraspecific competition. What is more controversial is whether mate choice can drive sympatric speciation by itself; that is, in the absence of disruptive selection, and we provide one example here. On the one hand, Higashi et al. (1999) argue that the runaway process of male secondary sexual trait evolution can by itself lead to the evolution of divergent female preferences and then to sympatric speciation. On the other hand, van Doorn et al. (2004) argue that the conditions promoting and maintaining this process are unlikely without some form of disruptive natural selection.

Competition in sympatric speciation models of sexual organisms has been modelled either with divergent environments (Doebeli, 1996; Kisdi & Geritz, 1999; Doebeli & Dieckmann, 2003) or without divergent environments (Dieckmann & Doebeli, 1999; Bolnick, 2006). Here, one conclusion has been that competition can drive sympatric speciation on an underlying unimodal resource distribution (Dieckmann & Doebeli, 1999) or a broad distribution of resources (Drossel & McKane, 2000), and that assortative mating seems to be a necessary part of this process. However, the importance of this competition-driven sympatric speciation remains controversial. For example, Polechová & Barton (2005) have argued that phenotypic clustering is only a transitory state driven by limits to the resource distribution, a conclusion that Doebeli et al. (2007) have since disputed.

Divergent environments are the original factor thought to drive sympatric speciation, that is, many classic models (Levene, 1953; Maynard Smith, 1962; Bush, 1975; Rice, 1984), as well as some recent ones (Fry, 2003; Gavrilets & Vose, 2005; Gavrilets et al., 2007), have shown that two specialist species can evolve in sympatry when two discrete resources are present, such as different host plants (Feder et al., 1994; Funk, 1998; Drès & Mallet, 2002; Nosil et al., 2002). A question that remains, however, is the importance of the degree of bimodality in relation to competition. Only one paper has examined

this question, and it suggested that resource bimodality leads to a more effective resource use at equilibrium (e.g. Doebeli, 1996).

We address the aforementioned issues through simulations in which we independently vary (i) the strength of mate choice that females exert on male foraging traits, (ii) the degree to which individuals with different phenotypes compete for resources and (iii) the extent to which resources are divergent (unimodal vs. increasingly bimodal resource distributions). We also consider the effects of the number of loci governing the foraging and mate choice traits. Our efforts are thus intended to produce a more integrated model of sympatric speciation that can simultaneously and formally consider the effects of multiple factors and their interactions.

Modelling framework

The model is an individual-based simulation that employs hard selection (Christiansen, 1975), realistic mutation rate (Dallas, 1992; Weber & Wong, 1993; Brinkmann et al., 1998), and the same modelling techniques as proposed by Gavrilets et al. (2007), Gavrilets & Vose (2009) and Thibert-Plante & Hendry (2011). The code is written in Fortran and is available upon request.

Environment

The environment is represented by a resource distribution. This distribution varies from unimodal to bimodal in shape, with the peaks separated by $\Delta\theta = \theta_2 - \theta_1$ with $\theta_{1,2}$ being the positions of the peaks and π controlling the relative height of each peak:

$$R'(x) = \pi \exp\left(-\frac{(x-\theta_1)^2}{2\sigma_R^2}\right) + (1-\pi)\exp\left(-\frac{(x-\theta_2)^2}{2\sigma_R^2}\right).$$
(1)

$R'(x)$ is normalized such that the total amount of resources is K_0 (carrying capacity) in the discrete form. The peaks are always symmetrically positioned around the centre of the possible resource distribution. Thus, an increasing distance between the peaks means an increasing resource 'valley' between the two peaks. The resource distribution is replenished at the start of each generation.

Individuals

The individuals are diploid hermaphrodites. They have different characters that are each controlled by L additive loci with three possible alleles at each locus ({−1,0,1}) as in the study by Thibert-Plante & Hendry (2011) and Gilman & Behm (in press). Each individual's foraging ability peaks at its foraging trait value (U) on the resource distribution, and each individual has a strength of mating preference (c) for that trait U. Thus, the value of c is used

to represent the strength of mate choice. The foraging trait U and mate choice c are genetically independent. To be concise, we refer to male, or female, when we talk about a characteristic that is expressed when the hermaphrodite individual acts as a male, or female, respectively. All the trait values are scaled to be between zero and one. The life cycle of individuals is (i) birth, (ii) foraging, (iii) viability selection and (iv) mating. Generations are nonoverlapping.

Foraging

The foraging ability ($F'(x)$) of an individual is a Gaussian function with a mean of U and standard deviation of σ_s:

$$F'(x) = \exp\left(-\frac{(x - U)^2}{2\sigma_s^2}\right). \quad (2)$$

Because of the genetic architecture described earlier, U can only take $4L + 1$ discrete values. We therefore normalize both the resource and the foraging functions to be non-null at those accessible $4L + 1$ values. The foraging ability ($F(x)$) of each individual is normalized to sum to one, whereas the resource distribution R sums to K_0 (maximum carrying capacity). σ_s specifies the competition factor among individuals with different foraging trait phenotypes: as σ_s increases, foraging ability overlaps more for a given trait difference and thus competition is greater among individuals with different phenotypes. We therefore refer to increasing σ_s as an increasing strength of competition (Table 1).

Viability selection

The viability of an individual is a function of its foraging ability and competition for resources. Each of the $4L + 1$ portions of the resource is shared among the individuals in the population, proportional to their foraging ability in that portion. The resources acquired on a specific resource type x ($\omega'_i(x)$) by an individual i with foraging ability F_i is the function of the number of individuals of all trait values n_j including its own n_i:

$$\omega'_i(x) = \frac{F_i(x)R(x)}{\sum_j n_j F_j(x)}. \quad (3)$$

This resource acquisition is then summed for an individual over the entire resource range to yield the total amount of resources acquired by that individual:

$$w_i = \sum_x w'_i(x). \quad (4)$$

The probability that an individual survives to the reproductive stage (v) is given then by a modified Beverton–Holt model (Kot, 2001):

$$v_i = \frac{\omega_i}{\omega_i + (b - 1)}, \quad (5)$$

where b is the average number of offspring produced by a female (Table 1).

Mate choice

Individuals who survive can then mate. Each surviving individual is chosen once as a 'female' and will produce on average b offspring, with the actual number produced for a given individual being drawn from a Poisson distribution. Every other surviving individual is a potential 'father' for the offspring of that female, and individual males can be chosen by more than one female. Males have the following probability of being chosen by a given female with U_2 and c (modified from the study by Bolnick (2004a, 2006)); Doebeli (2005) by Gavrilets *et al.* (2007):

$$\Psi(U_1, U_2, c) = \begin{cases} \exp\left[-(2c - 1)^2 \frac{(U_1 - U_2)^2}{2\sigma_a^2}\right], & \text{if } c \geq 0.5 \\ \exp\left[-(2c - 1)^2 \frac{(U_1 - (1 - U_2))^2}{2\sigma_a^2}\right], & \text{if } c < 0.5. \end{cases} \quad (6)$$

At $c = 0.5$, every male has the same probability of being chosen, and so mating is random. At $c > 0.5$, positive assortative mating occurs based on the foraging trait (U). At $c < 0.5$, negative assortative mating occurs based on the same foraging trait. σ_a scales the strength of the preference as a function of U_1 and U_2. As σ_a decreases, females are more selective. For all simulations, c and σ_a are fixed parameters, except for a series of simulations where c evolves (Table 1).

Initial conditions

The loci controlling the ecological trait (U) initially have an equal probability of having values $\{-1, 0, 1\}$. As a result, the average individual at the start of the simulation has a phenotype that is at the centre of the resource distribution. All loci have the same mutation probability of 10^{-5} (which is similar to that in the study by Dallas,

Table 1 Parameter space explored.

Parameter	Symbol (if any)	Values
Strength of preference	c	{0.3,0.5,0.6,0.7,0.8,0.9,evolvable}
Distance between the peaks	$\Delta\theta$	{0,0.2,0.4,0.6,0.8,1}
Scaling factor of the mating preference	σ_a	{0.083,0.167,0.24,0.333}
Competition between phenotypes	σ_s	{0.001,0.083,0.167,0.24,0.333,1000}
Resource distribution width	σ_R	{0.042,0.083,0.167,0.24,0.333,1000}
Maximum carrying capacity	K_0	{2048,4096}
Number of loci per trait	L	{4,8}
Average number of offspring	b	{3}
Relative magnitude of the resource peak	π	{0.5}

1992; Weber & Wong, 1993; Brinkmann et al., 1998; Gavrilets & Vose, 2005). This initial condition provides enough variability to allow the persistence of the population even if the population average phenotype is initially in a resource gap. For this reason, our model initially represents a generalist species occupying a new environment that might or might not have two resources that specialists might occupy. If we had instead modelled a single specialist species adapted to one environment before adding a second environment, sympatric speciation would probably have been less likely. Mutations increase or decrease the locus value by one, with equal probability and have reflective boundaries at −1 and 1 as in other models (Thibert-Plante & Hendry, 2011; Gilman & Behm, in press). Initially, the population is at carrying capacity. Table 1 lists the parameter space explored in the simulations. All combinations are run for 2000 generations, which was sufficient to reach stability, with ten replicates for each parameter combination. For simulation where mating preference evolved, we started the simulations with monomorphic value of mating preference $c = 0.5$. The loci controlling c have the same number of loci and the same mutation rate as the ecological trait (U). Since the nature of the simulations where mating preference evolved, we analysed them separately in most cases.

Tracking

We use an integrative approach where three main independent axes are considered for their effects on sympatric speciation. The first axis is the degree of competition among individuals with different phenotypes, and the standardized measure for this is σ_s. The second axis is the degree of mate choice. Here we use the standard deviation of the standardized mating preference function ($\frac{1}{M} \int \Psi(U1, x, c) dx = 1$), where M is the normalization factor:

$$sdSex = \frac{\sigma_a}{abs(1 - 2c)}. \tag{7}$$

As $sdSex$ increases, mating becomes less random. The last axis is resource shape. Here we calculate the amount of resources from one peak (θ_1) that are present at the centre of the other peak ($U_2 = \theta_2$):

$$shape = \exp\left(-\frac{\Delta\theta^2}{2\sigma_R^2}\right). \tag{8}$$

Formally, we shift from a cumulative unimodal resource distribution to a bimodal resource distribution when $(\Delta\theta)^2$ becomes larger than $4\sigma^2$. In terms of *shape*, this transition occurs when it goes below e^{-2}. *Shape* captures more than just the transition point, as *shape* decreases, bimodality gets stronger.

We look at the effects of competition, mate choice and resource shape on adaptation and the number of intermediate forms, which include hybrids (see Results).

Adaptation is measured as the population size after reproduction and is normalized by the carrying capacity, that is, our measure of adaptation is overall system-wide adaptation: the ability of the system to convert the entire resource distribution into reproductive individuals. For hybridization, we calculate the deviation from the random expectation (no natural selection, no mate choice and no competition, i.e. random distribution of allele at each loci given our mutation scheme) of the number of individuals at the centre of the resource distribution, $-\frac{\sigma_s}{2} \leq U \leq \frac{\sigma_s}{2}$, hereafter called 'intermediate individuals'. The criterion for intermediate individuals is thus normalized by the foraging range of the individuals.

Results

Extinction occurred in 474 of the 241 920 simulations (0.2%). All of these extinctions occurred when both the foraging range of individuals was the smallest ($\sigma_s = 0.001$) and the distance between the resource peaks was large ($\Delta\theta > 0.6$). In these cases, a wide and deep fitness valley was present between the two resource peaks and this valley could not be bridged by an individual, because foraging was too specialized. Because our simulations started with a population having phenotypes in the centre of the resource distribution, these conditions sometimes made it impossible to colonize either resource peak, causing system-wide extinction. The simulations leading to extinction were excluded from the following analyses.

The overall results are shown in a phase plane (Fig. 1a, Table 2) representing (i) the overall level of system-wide adaptation (actual population size divided by the total carrying capacity) and (ii) the number of intermediate individuals ($-\frac{\sigma_s}{2} \leq U \leq \frac{\sigma_s}{2}$) relative to those expected under the null scenario (see Tracking in the Methods). We define four zones on this phase plane (Fig. 1).

Zone 0 (upper left): adaptation is very high (≥ 0.7) and intermediates are very rare (≤ 0.01). This zone represents cases of full sympatric speciation (FSS), where two phenotypic clusters are present and hybridization between them is very rare (Fig. S1 for an example).

Zone 1 (upper centre): adaptation is high (≥ 0.7) and intermediates are more common than in Zone 0 but still notably fewer than expected under the null scenario (0.01 < intermediates <0.6). This zone represents cases of progress towards, but not the attainment of, full sympatric speciation (PTSS) (Fig. S2 for an example).

Zone 2 (upper right): adaptation is high (≥ 0.7) and intermediates are common (> 0.6). In this case, a large number of individual specialists are distributed across the resource range, or more rarely, a single generalist population is present (Fig. S3 for an example).

Zone 3 (lower): adaptation is low and intermediates are few. This zone includes cases where only one of the two existing resource peaks is occupied, that is, the
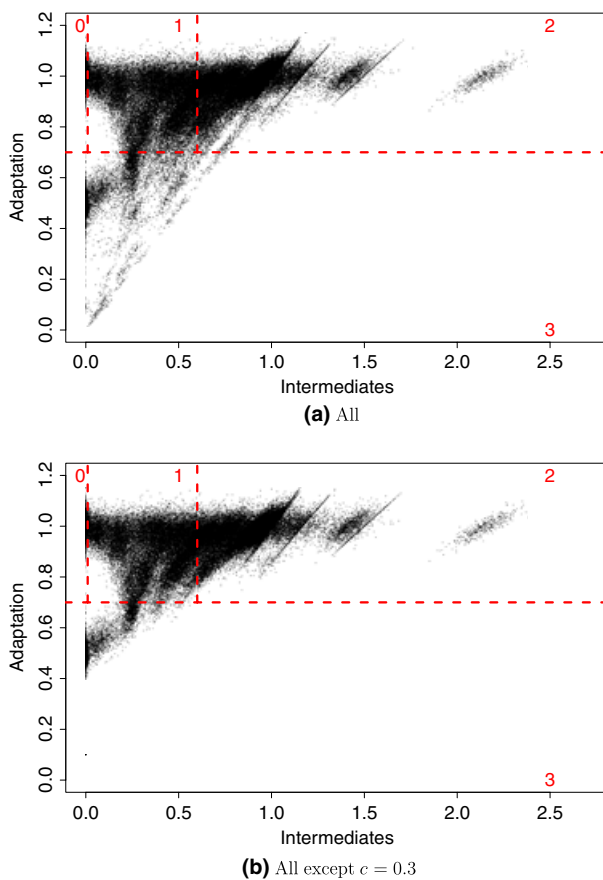
(a) All

(b) All except $c = 0.3$

Fig. 1 (a) Phase plane of all the simulations. (b) Phase plane of all simulations except those with negative assortative mating (all except $c = 0.3$, it is worth noting that $c = 0.3$ is the only value below 0.5 that was tested). Each simulation is represented by its adaptation (system-wide population size divided by the maximum carrying capacity) and its level of hybrids (number of hybrids observed divided by the number expected without competition, natural selection or mate choice).

population is specialized on one of the two available resources, whereas the other is not exploited (Fig. S4 for an example). This zone also includes cases where

adaptation is not achieved because negative assortative mating strongly homogenizes the gene pool and prevents specialists from efficiently exploiting the resource distribution.

In the following sections, we first consider the influence of each main factor of interest while ignoring variation in the other factors (i.e. summing across all runs for a given level of the factor of interest). We then examine interactions among the factors.

Factors determining progress towards sympatric speciation

With no mate choice ($c = 0.5$, $sdSex = \infty$), we never recorded an instance of full sympatric speciation (FSS, Zone 0), and we saw only a few instances of progress towards sympatric speciation (PTSS, Zone 1). Although some cases of high adaptation and few intermediates were evident (Fig. 2a, Table 2), these cases were not accompanied by phenotypic bimodality. Instead, there is a reduction in adaptation as the intermediates decrease, because only one type of specialist evolved. With strong assortative mating ($sdSex < \frac{1}{3}$), FSS and PTSS were more common (Fig. 2b, Table 2), although these outcomes still occured in only about 14% and 27% of the simulations, respectively. Factors other than mate choice are clearly influencing progress towards sympatric speciation, as the following sections will make clear.

With strong competition among different phenotypes ($\sigma_s \geq \frac{1}{3}$), strong maladaptation (Zone 3) never occurred (Fig. 3a), but both FSS and PTSS were rare (Table 2). This was because all individuals could, at least to some extent, use the entire resource range irrespective of their phenotype. In this case, there is no frequency dependance selection, because individuals are generalist, but density dependance selection. With weak competition among different phenotypes (i.e. high specialization, $\sigma_s < 0.1$), cases of maladaptation (Zone 3) were increasingly common (Fig. 3b). These situations occurred when a population of individuals specialized first on one peak and, for that reason, could not then colonize the second peak. Zone 3 also includes some cases of negative assortative mating (Fig. 1b) or random mating (no mate

Table 2 Percentage of simulations ending in each of the four zones (Fig. 1). FSS and PTSS represent full sympatric speciation and progress towards sympatric speciation, respectively. All simulations combined include the evolvable c and the negative assortative mating.

| Condition	Symbol (if any)	Zone 0 (FSS)	Zone 1 (PTSS)	Zone 2	Zone 3
All simulations combined		3.47	18.41	71.84	6.28
Random mating	($c = 0.5$)	0.00	11.96	77.06	10.98
Strong assortative mating	($sdSex < \frac{1}{3}$)	13.89	27.13	58.84	0.14
Strong competition	($\sigma_s \geq \frac{1}{3}$)	1.14	0.19	98.67	0.00
Weak competition	($\sigma_s < 0.1$)	2.79	48.30	30.81	18.10
Unimodality	(shape $> \frac{2}{3}$)	0.78	17.02	79.91	2.29
Bimodality	(shape $\leq \frac{1}{3}$)	5.46	19.63	65.62	9.29
Evolving c		0.30	13.41	75.63	10.66
Negative assortative mating	($c = 0.3$)	0.00	6.00	79.90	14.10
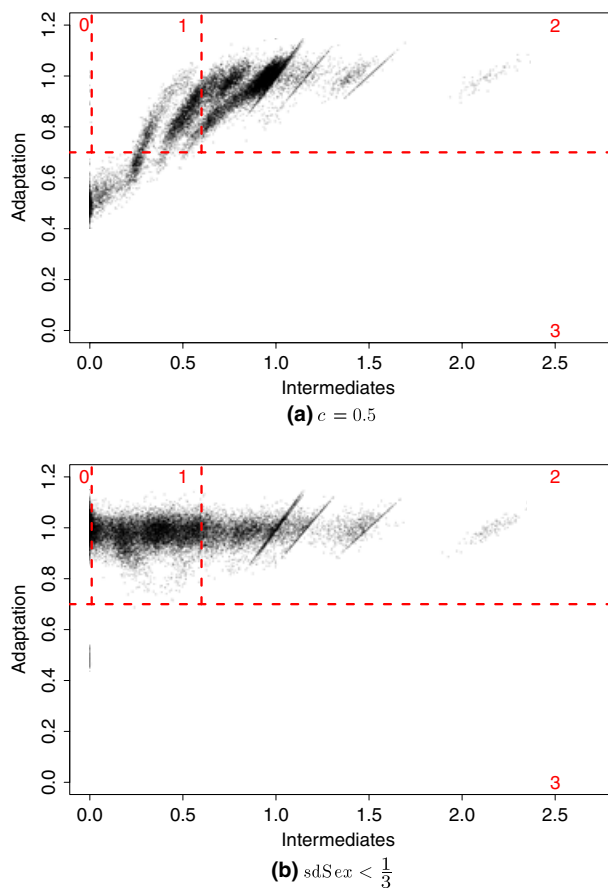
Fig. 2 (a) Phase plane of simulations without mate choice ($c = 0.5$). (b) Phase plane of simulations with strong mate choice ($sdSex < \frac{1}{3}$). See Fig. 1 for the definition of the axis.

Fig. 3 (a) Phase plane of simulations with strong competition among different phenotypes ($\sigma_s > \frac{1}{3}$). (b) Phase plane of simulations with weak competition among different phenotypes ($\sigma_s < 0.1$). See Fig. 1 for the definition of the axis.

choice), in which gene flow prevented adaptive divergence. Weak competition also led to some cases of FSS (3%) and PTSS (48%) (Table 2). The reason was that different populations of individuals could specialize on alternative resources.

With resource unimodality ($shape > \frac{2}{3}$), strong maladaptation almost never occurred (Fig. 4a, Table 2), because nothing prevented adaptation to the single resource peak. FSS sometimes occurred, but these cases were rare (Table 2). With strong resource bimodality ($shape \leq \frac{1}{3}$), FSS was more common (5%) and PTSS remained about the same (20%) (Table 2).

Interactions and other potential influences

As the foregoing summary reveals, mate choice, competition and resource distributions all contribute to FSS and PTSS. However, the percentage of simulations that achieved FSS was never very high for a given level of any factor of interest (Table 2). This suggests the presence of other limits on progress towards sympatric speciation.
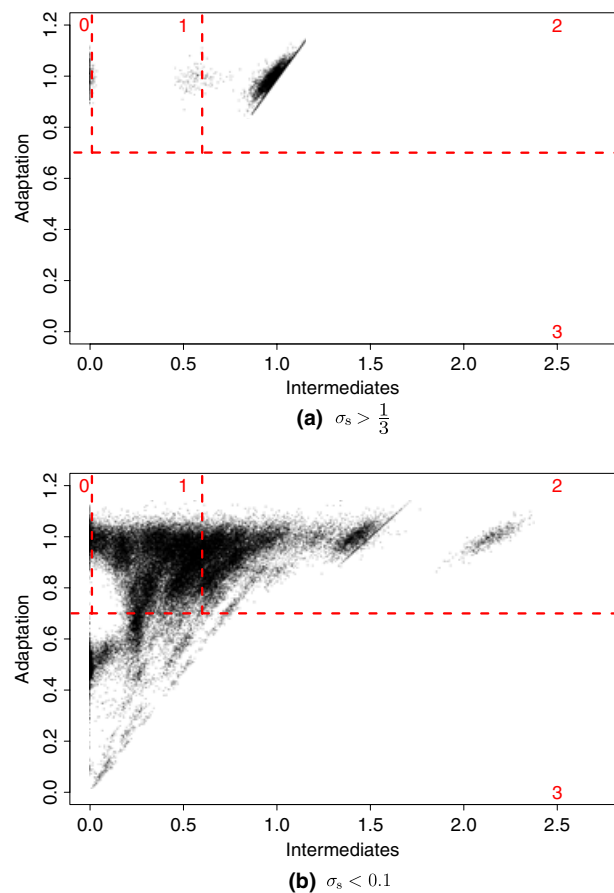
One of these limits involves interactions among the three factors on which we focused. In particular, almost all (91.52%) cases of FSS occurred when mate choice was strong and resources were strongly bimodal (Fig. 6, Table 3). Under these conditions, gaps in the resource distribution lead to specialist individuals exploiting each resource peak, which are therefore incapable of exploiting alternative resource peaks. This disruptive selection then drives the evolution of mating isolation between populations using those different resources. The only other condition allowing a substantial number of FSS cases entailed strong mate choice, low bimodality in the resource distribution, and intermediate competition among different phenotypes. These situations parallel those described by Dieckmann & Doebeli (1999) and Drossel & McKane (2000).

In addition to interactions among the three key factors described earlier, other factors might also influence progress towards sympatric speciation, for instance we found that the maximum carrying capacity (K_0) had no

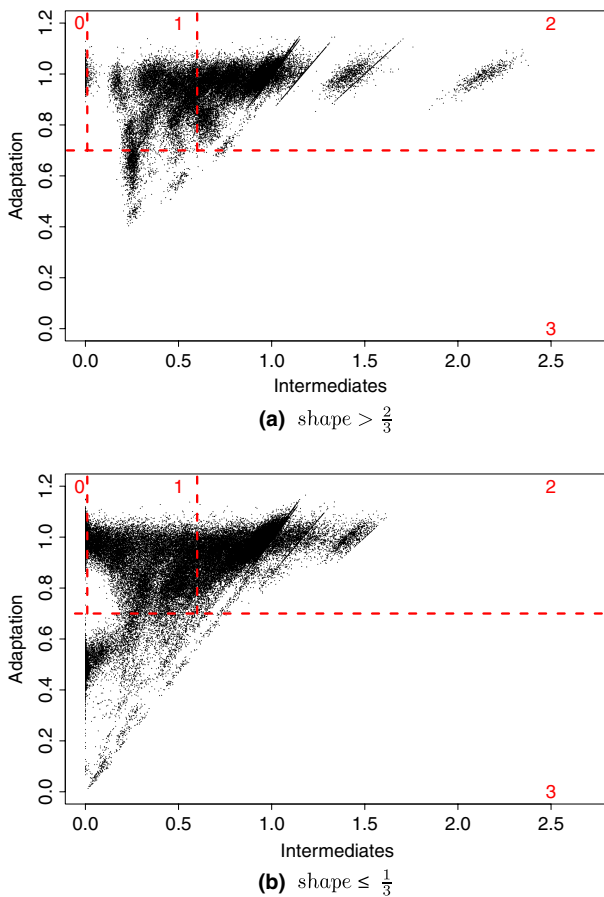**(a)** $shape > \frac{2}{3}$

(b) $shape \leq \frac{1}{3}$

Fig. 4 (a) Phase plane of all unimodal simulations ($shape > \frac{2}{3}$). (b) Phase plane of simulations with strong bimodality ($shape \leq \frac{1}{3}$). See Fig. 1 for the definition of the axis.

(a) Evolved $\bar{c} - \mathrm{sd}(c) > 0.5$
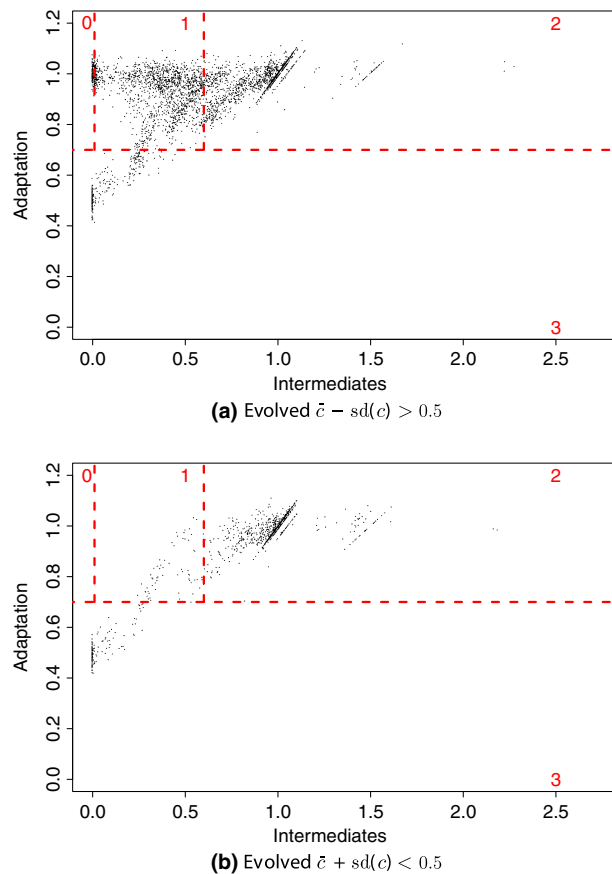

(b) Evolved $\bar{c} + \mathrm{sd}(c) < 0.5$

Fig. 5 (a) Phase plane of simulations that evolved positive assortative mating. (b) Phase plane of simulations that evolved negative assortative mating. See Fig. 1 for the definition of the axis.

influence, but a larger number of loci controlling the trait slightly reduced the number of cases of FSS (3.2% vs. 3.7%). This result is consistent with the models proposed by Gourbiere (2004), Gavrilets (2004), Bürger *et al.* (2006), Gavrilets *et al.* (2007), Gavrilets & Vose (2007, 2009), and Thibert-Plante & Hendry (2011), who all found that fewer loci increase the likelihood of speciation. However, the importance of this effect seems much lower in our model than in those analysed previously.

The previously described scenarios all used a constant value for mating preference (c) throughout each run. As the initial level of preference can influence population divergence (Kirkpatrick & Ravigné, 2002), the *evolution* of mating preference (c) from random mating is also considered. When allowing the potential for this evolution, we found that mate choice did not evolve in most of the simulations in which its evolution was permitted, like in the study by Labonne & Hendry (2010) and Thibert-Plante & Hendry (2011). That is, only 13% the time did the population starting at $c = 0.5$ later evolve a c with a standard deviation that did not overlap the starting point.

Of those 13% of cases, most (73%) represented the evolution of positive assortative mating with respect to phenotype (c significantly >0.5). Stronger positive assortative mating tended to evolve when the preference range (σ_A) was narrow, competition was strong (σ_R larger) and the distance between the peaks ($\Delta\theta$) was larger. When it did evolve, the strength of preference sometimes became high (as much as $c = 0.97$ under the favourable conditions described earlier), but the average was around $c = 0.6$. Both a smaller carrying capacity and large number of loci controlling each trait led to fewer simulations evolving assortative mating. Only a few simulations where mate choice evolved from a starting point of $c = 0.5$ led to FSS (Table 2 and Fig. 5).

Even if simulated data should be analysed like empirical data (Winsberg, 2003), the nonstatic nature of simulated data and the artificially controlled number of replicates (Grimm & Railsback, 2005) dictate that the statistical results should be interpreted with caution. For those interested in statistical analyses, we present ANOVA results in Tables S1 and S2. As can be seen, these analyses support our assertions that mate choice,
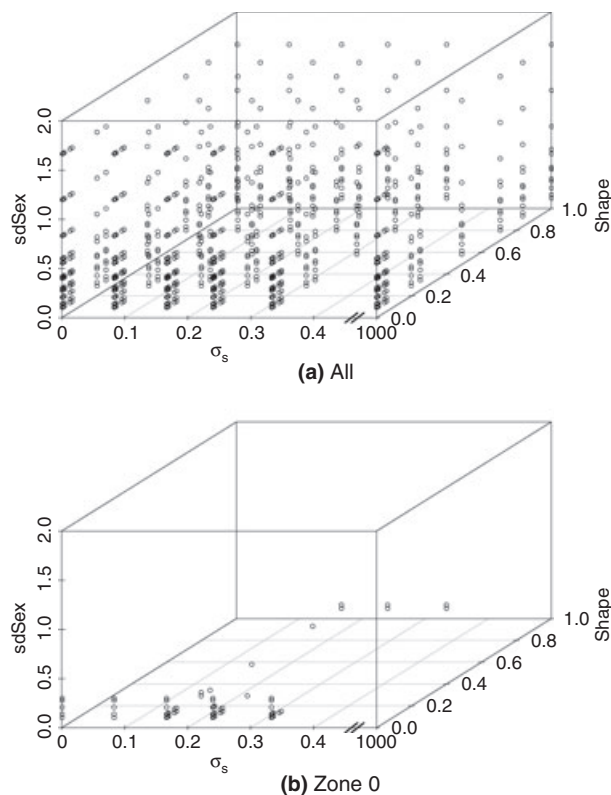
Fig. 6 All simulations done (a) and those falling in Zone 0 FSS (b).

Table 3 Percentage of simulations ending in full sympatric specia-tion (FSS: Zone 0 in the figures) for different parameters. In parenthes is the percentage of simulations for each parameter combination that ended in Zone 0 FSS, i.e. similar to the other value, but without normalization. For competition, we define weak ($\sigma_s < 0.1$), intermediate ($0.1 \geq \sigma_s < \frac{1}{3}$) and strong ($\sigma_s \geq \frac{1}{3}$). For bimodality, we define low ($shape > \frac{2}{3}$), medium ($\frac{1}{3} < shape \leq \frac{2}{3}$) and high ($shape \leq \frac{1}{3}$). All values for weak levels ($sdSex \geq \frac{2}{3}$) and intermediate levels ($\frac{1}{3} \leq sdSex < \frac{2}{3}$), of mate choice were 0.00, so only values for strong mate choice ($sdSex < \frac{1}{3}$) are shown.

Bimodality	Low	Medium	High
Weak competition	0.00 (0.00)	0.00 (0.00)	26.70 (19.17)
Intermediate competition	7.43 (8.56)	0.33 (2.50)	54.56 (38.92)
Strong competition	0.72 (0.83)	0.00 (0.00)	10.25 (7.31)

competition, and the shape of the resource distribution are all influencing sympatric speciation along the full set of their interaction. Moreover, the results support our above assertions about the relative strength of different factors on the probability of sympatric speciation.

Discussion

A large number of theoretical models have examined the conditions that promote or constrain ecologically based sympatric speciation (e.g. Doebeli, 1996; Dieckmann & Doebeli, 1999; Doebeli & Dieckmann, 2000; Drossel & McKane, 2000; Doebeli & Dieckmann, 2003; Polechová & Barton, 2005; Bürger et al., 2006; Doebeli et al., 2007). Few of these studies, however, consider three key effects together: mate choice, competition and the shape of the resource distribution (unimodal through varying degrees of bimodality). By explicitly adopting this more inte-grated approach, we address the likelihood that each factor is necessary and/or sufficient, whether individually or in combination, for sympatric speciation.

Mate choice has long been considered an important part of sympatric speciation, because it allows for the evolution of positive assortative mating. Without assor-tative mating, populations occupying a diversity of resources become homogenized (Kirkpatrick & Nuismer, 2004). We confirmed this result: sympatric speciation never occurred when mate choice was absent, regardless of the nature of competition and the shape of the resource distribution (Tables 2 and 3). In sexual organ-isms, then, mate choice could often be necessary for sympatric speciation. Exceptions will occur when other means of generating positive assortative mating are present, such as habitat choice (Feder et al., 1994; Nosil et al., 2002) or differences in reproductive timing (Hendry & Day, 2005; Savolainen et al., 2006; Devaux & Lande, 2008). But is mate choice sufficient by itself for sympatric speciation? Some models have argued that it is (Higashi et al., 1999), whereas most have argued that it is not (Arnegard & Kondrashov, 2004; Gourbiere, 2004; van Doorn et al., 2004). In general, it seems that mate choice must be coupled to adaptive divergence. We also confirm this assertion because mate choice, even when strong, never caused speciation unless disruptive selec-tion was present due to either a bimodal resource distribution or competition. We thus add our voice to those arguing that mate choice, or some other assortative mating mechanism is normally necessary but not suffi-cient for sympatric speciation in sexual organisms.

Competition on a single unimodal resource distribu-tion has been argued by some authors to drive sympatric speciation (Doebeli, 1996; Dieckmann & Doebeli, 1999; Bürger et al., 2006). Other authors, however, have argued that this result is extremely rare and only found under a very limited, and potentially unrealistic, param-eter range (Gavrilets, 2005; Polechová & Barton, 2005). Our results support both assertions. First, we found that sympatric speciation can indeed occur on strictly unimo-dal resource distributions (Fig. 4a). However, we also found that this result occurred in < 1% of the simulations under those conditions (Table 2) and only when mate choice was strong (as above) and (predominantly) at intermediate levels of competition between different phenotypes (Table 3). In those cases competition was strong enough to induce disruptive selection, but not strong enough to cause competitive exclusion. Even here, however, sympatric speciation was not very

common, reinforcing the important stochastic element to sympatric speciation by competition.

Divergent environments are thought to be an important contributor to sympatric speciation, for example, many radiations of insects involve divergence onto different host plants (Feder *et al.*, 1994; Funk, 1998; Drès & Mallet, 2002; Nosil *et al.*, 2002) but less commonly on the same host plant. Exceptions to the latter statement occur in the case of specialization on different plant parts or through different reproductive timing (e.g. Joy & Crespi, 2007). In most cases, then, adaptive radiation generally involves specialization on resources or environments that are at least somewhat distinct (or discrete), as opposed to the partitioning of a single unimodal resource. Moreover, classic models confirm the relative ease with which two specialists evolve in an environment with two discrete resources (e.g. van Tienderen, 1991; Fry, 2003; Ackermann & Doebeli, 2004). Our results confirm that divergent environments are an important promoter of sympatric speciation. In most previous models, this speciation occurred through the evolution of host preference that resulted in reduced gene flow between groups (e.g. Fry, 2003; Gavrilets & Vose, 2005; Gavrilets *et al.*, 2007). In our model, however, it was the result of mate choice, further extending the conditions under which divergent environments can drive sympatric speciation. However, even strongly bimodal resource distributions did not inevitably cause sympatric speciation. Instead, mate choice was also necessary and intermediate levels of competition among phenotypes was helpful. Even under these conditions, sympatric speciation occurred less than 40% of the time (Table 3). The other 60% of these simulations led to either incomplete resource use (low overall adaptation) or different individuals spread across the entire resource range (a population composed of a diverse array of individual specialists). However, even under the most conducive conditions, sympatric speciation often did not occur. This reminds us of the stochastic nature of sympatric speciation even under optimal conditions.

Interactions and extensions

A key feature of our results was that the mate choice, the nature of competition, and the shape of the resource distribution strongly interact to influence progress towards sympatric speciation. Thus, one might say that competition on unimodal distributions can indeed generate speciation, but it is also fair to say that bimodal distributions make it much easier (Doebeli, 1996); for instance, as the resources distribution becomes increasingly bimodal, sympatric speciation occurs more easily at all levels of competition. On the one hand, neither competition nor resource bimodality can drive sympatric speciation on their own; mate choice that reduces gene flow between diverging groups is also necessary. On the other hand, mate choice alone (with low competition

and unimodal resource distribution) was not sufficient to reduce the number of intermediates at the centre of the resource distribution without stronger disruptive selection cause by competition or, especially, resource bimodality.

As an important qualifier, our simulations started with phenotypes in the centre of the resource distribution, equidistant between the two peaks. Sympatric speciation would probably be less likely if we had started with a population well adapted to one resource and then introduced a second resource. The reason is that individuals specializing on a single resource peak will have difficulty using, and therefore colonizing, a second resource peak. Here might be a situation where increasing resource bimodality decreases the likelihood of sympatric speciation, as has been shown in parapatric models (Thibert-Plante & Hendry, 2009).

We feel that the best insights into factors influencing sympatric speciation are not derived from studies that examine only one or a few primary factors. Instead, the relative importance of different factors and their interactions can be revealed only by more inclusive models. To our existing framework, it would therefore seem appropriate to incorporate even more factors, such as habitat preference (Fry, 2003; Gavrilets *et al.*, 2007; Gavrilets & Vose, 2007), for example, habitat preference might reinforce assortative mating and ease sympatric speciation. At the same time, it might weaken the importance of mate choice acting towards the same end.

Finally, we modelled the evolution of a foraging trait by changing only the position of the centre of an individual's foraging ability on the resource distribution. It would therefore be useful to also allow the *evolution* of generalist vs. specialist foragers (van Tienderen, 1991; Ackermann & Doebeli, 2004). This would entail allowing the width of the foraging distribution of individuals to evolve independently of its central value. This method was employed in studies of generalist vs. specialist populations (van Tienderen, 1991; Ackermann & Doebeli, 2004), but not in the context of comparing the relative strength of various promoters of sympatric speciation on a bimodal resource distribution. In short, many opportunities exist for further integrative simulation models to explore the factors and interactions that promote or constrain sympatric speciation.

We close with a discussion about the relevance of our results and related modelling efforts by others to inferences about real biological diversity. First, although sympatric speciation was rare in our models (3.5% of all simulations), this would still suggest that sympatric speciation is important, that is, if 3.5% (or whatever other precentage) of all populations sympatrically speciate in < 2000 generations, then sympatric speciation should be very common in nature. This then leads to our second main point: sympatric speciation seems much easier in models than in nature. Few people now question that sympatric speciation has occurred in nature

(Bolnick & Fitzpatrick, 2007), but few people also believe that it has been very common. Thus, even models that suggest sympatric speciation can occur only sometimes are clearly generating something that is not that frequent in nature. This discrepancy could occur because the conditions simulated in models are rare in nature (e.g. we started our simulations with individuals intermediate between two resource distributions) or because other interacting factors have not been fully considered (e.g. temporal variation). Although much more work can be carried out with sympatric speciation models, the incorporation of at least some spatial structure (Fitzpatrick et al., 2008; Thibert-Plante & Hendry, 2009) is undoubtedly a more productive way to generate insights into the majority of real biological diversity.

Acknowledgments

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Table S1 ANOVA table of the factors influencing adaptation.

Table S2 ANOVA table of the factors influencing the number of intermediates.

Figure S1 Supporting information: Zone 0 example with ($c = 0.9$, $\Delta\theta = 1.0$, $\sigma_a = 0.24$, $\sigma_s = 0.24$, $\sigma_R = 0.083$, $K_0 = 4096$, $L = 8$).

Figure S2 Supporting information: Zone 1 example with ($c = 0.9$, $\Delta\theta = 1.0$, $\sigma_a = 0.333$, $\sigma_s = 0.083$, $\sigma_R = 0.167$, $K_0 = 4096$, $L = 8$).

Figure S3 Supporting information: Zone 2 example with ($c = 0.9$, $\Delta\theta = 1.0$, $\sigma_a = 0.333$, $\sigma_s = 0.167$, $\sigma_R = 0.333$, $K_0 = 4096$, $L = 8$).

Figure S4 Supporting information: Zone 3 example with ($c = 0.7$, $\Delta\theta = 1.0$, $\sigma_a = 0.333$, $\sigma_s = 0.083$, $\sigma_R = 0.042$, $K_0 = 4096$, $L = 8$).

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