SHORT COMMUNICATION
Refining the conditions for sympatric ecological speciation

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Abstract

Can speciation occur in a single population when different types of resources are available, in the absence of any geographical isolation, or any spatial or temporal variation in selection? The controversial topics of sympatric speciation and ecological speciation have already stimulated many theoretical studies, most of them agreeing on the fact that mechanisms generating disruptive selection, some level of assortment, and enough heterogeneity in the available resources, are critical for sympatric speciation to occur. Few studies, however, have combined the three factors and investigated their interactions. In this article, I analytically derive conditions for sympatric speciation in a general model where the distribution of resources can be uni- or bimodal, and where a parameter controls the range of resources that an individual can exploit. This approach bridges the gap between models of a unimodal continuum of resources and Levene-type models with discrete resources. I then test these conditions against simulation results from a recently published article (Thibert-Plante & Hendry, 2011, *J. Evol. Biol.* **24**: 2186–2196) and confirm that sympatric ecological speciation is favoured when (i) selection is disruptive (i.e. individuals with an intermediate trait are at a local fitness minimum), (ii) resources are differentiated enough and (iii) mating is assortative. I also discuss the role of mating preference functions and the need (or lack thereof) for bimodality in resource distributions for diversification.

Introduction

Whether a new species can evolve from a single ancestor species, in the absence of any sort of geographical isolation [i.e. a geographical definition of sympatric speciation (Fitzpatrick *et al.*, 2008)] is a central but also controversial question in evolutionary biology (Gavrilets *et al.*, 2007). Beyond the geographical context in which speciation occurs, emphasis has also been laid on which mechanisms drive speciation (The Marie Curie SPECIATION Network, 2012). Schluter (2001) identified four – non mutually exclusive – modes of specia-

tion, depending on what causes the initial divergence in the population: (i) ecological speciation, due to ecologically based divergent selection (Schluter & Conte, 2009); (ii) divergence under uniform selection, which includes in particular speciation by sexual conflict (Gavrilets & Waxman, 2002); (iii) speciation by drift (Higgs & Derrida, 1991, 1992); and (iv) speciation involving polyploidy. In this article, I focus on the first mode, ecological speciation, which by definition requires divergent ecologically based selection. Specifically, I consider ecological speciation occurring in sympatry, a situation similar to what is referred to as adaptive speciation (Dieckmann *et al.*, 2004).

A plethora of theoretical models have already been proposed to study speciation (Kirkpatrick & Ravigné, 2002), a substantial number of the most recent ones relying on massive computer simulations. In a recent study, Thibert-Plante & Hendry (2011) (hereafter TPH) used an integrative simulation approach to identify the

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factors promoting sympatric speciation, examining the combined influences of mate choice, competition for resources and resource diversity. In their model, mate choice occurs via magic traits (Servedio *et al.*, 2011): a mate is chosen on the basis of the ecological trait under selection. Competition is modelled through differential foraging abilities (instead of direct competition); when the range of resources that can be exploited by an individual is larger, this individual can access more resources, but at the same time has to compete for them against more individuals. The main originality of TPH's model is the way resources are modelled: a continuum of different resources is present, their distribution ranging from strictly unimodal to bimodal. Previous studies had either focused on a unimodal continuum of resources (e.g. Roughgarden, 1979; Doebeli & Dieckmann, 2000) or on discrete bimodal niches (Levene-type models) (but see Doebeli, 1996). In their analysis, however, TPH investigated the role of competition for resources independently of the actual shape of the distribution of resources. Presenting a detailed analysis of the 'ecological' counterpart of TPH's model (i.e. a model with clonal reproduction of the different phenotypes), I show in this article that the interaction between competition for resources and the shape of the resource distribution determines whether or not natural selection is divergent, and whether the resources are enough differentiated. These are conditions that need to be met for the maintenance of distinct clades or clusters of species, and these conditions therefore represent favourable conditions for sympatric speciation to occur in a sexual model. With this analytical insight, I suggest new axes for analysing TPH's simulated data. In the course of the analysis, I also discuss the choice of functions for modelling assortative mating.

Model

I model a population living in an environment where different types of resources are available. I write $R(x)$ the relative abundance of resource x. I assume that $R(x)$ is the weighted sum of two Gaussian distributions, with maxima at θ_1 (representing a proportion q of the total resources) and $\theta_2 = \theta_1 + \Delta\theta$ (in proportion $1-q$) respectively, and with the same widths σ_R (see the filled grey curves on Fig. 1b–f, drawn with $q = 1/3$):

$$R(x) = \frac{1}{\sigma_R\sqrt{2\pi}}\left[q\exp\left(-\frac{(x-\theta_1)^2}{2\sigma_R^2}\right) + (1-q)\exp\left(-\frac{(x-\theta_2)^2}{2\sigma_R^2}\right)\right] \quad (1)$$

The mean resource type is therefore $\bar{x} = q\theta_1 + (1-q)\theta_2$.

The foraging ability of individuals with a foraging trait U on resources x, $F(U,x)$, is a Gaussian-shaped function peaking at $x = U$ (the preferred resource), and of width σ_S (measuring the range of resources that can be exploited, and the same for all individuals) (Thibert-Plante & Hendry, 2011):

$$F(U,x) = \exp\left(-\frac{(x-U)^2}{2\sigma_S^2}\right) \quad (2)$$

Following TPH, I assume that the share of resource x that an individual with trait U can exploit, $\omega(U,x)$ is proportional to the relative foraging efficiency of this individual with trait U, compared with the whole population. Letting $p_t(V)$ equal the frequency of individuals with trait V at time t, we have:

$$\omega(U,x) = \frac{F(U,x)}{\int_{-\infty}^{+\infty} F(V,x)p_t(V)\mathrm{d}V} \quad (3)$$

The fitness of individuals with trait U, $w(U)$, is then obtained by integrating $\omega(U,x)$ over the whole range of available resources, taking their distribution $R(x)$ into account:

$$w(U) = \int_{-\infty}^{+\infty} \omega(U,x)R(x)\mathrm{d}x \quad (4)$$

The fitness of an individual is therefore highly frequency-dependent: the share of resources this individual can exploit depends on the composition of the whole population. What matters for gathering resource x is not the absolute foraging efficiency of an individual, but its *relative* foraging efficiency.

Finally, in my analysis, population sizes are presumed to be big enough for drift to be negligible.

Results

In the course of the analysis of the model, I will define three axes, corresponding to three conditions for sympatric speciation along which I will then reanalyse TPH's data. The names of the three conditions (X, Y, Z) refer to their localization as axes in Fig. 3a. One axis (Y) corresponds to the disruptiveness of ecologically based selection (i.e. whether intermediate traits correspond to a local fitness minimum (Anonymous, 2001), here equivalent to whether the variance of the distribution of phenotypes can be larger after selection than before, a condition which is absent from TPH's analysis). Another axis (X) is related to the heterogeneity of resources (which is different from TPH's). These two first axes are combined into a χ axis on Fig. 3b; finally the last axis (Z) is for assortment (almost the same as TPH).

Conditions for disruptive selection

I first focus on the 'ecological' counterpart of the sexual model: I assume that individuals with different preferred resources U belong to different species, and
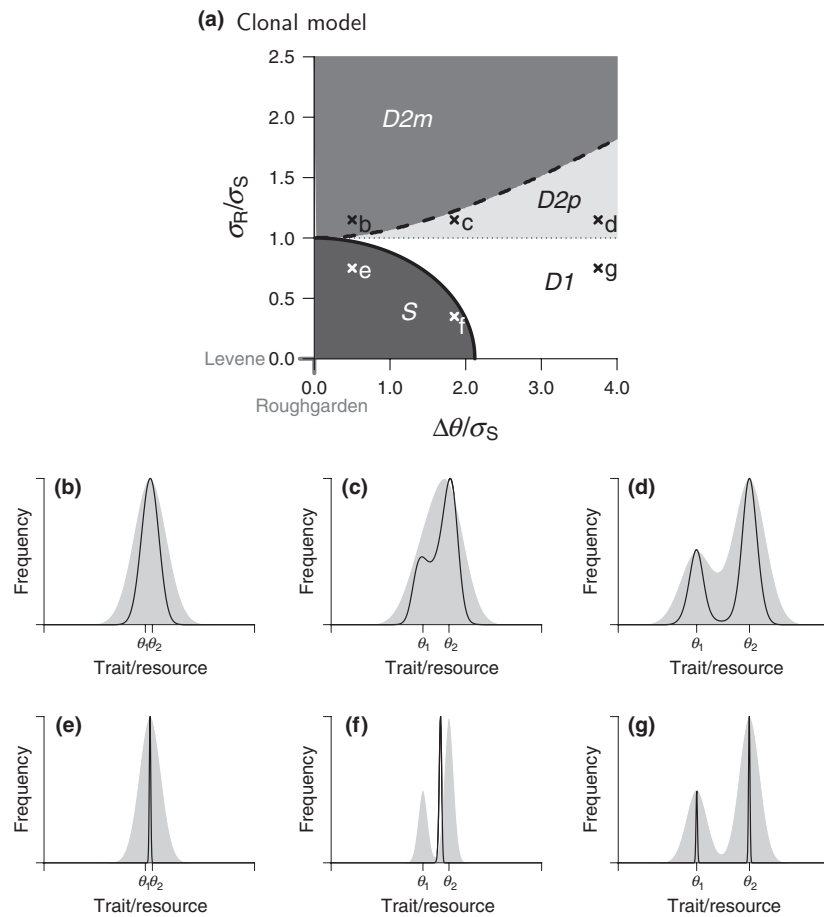
Fig. 1 (a) Conditions for diversification and bimodality in the ecological model, for different distances between the resource peaks ($\Delta\theta/\sigma_S$), and relative width of the resource functions (σ_R/σ_S); the resource centered at θ_1 represents $q = 1/3$ of the total resources. Black area S: locally stabilizing selection, no diversification is possible; $D1$, $D2p$, $D2m$: locally disruptive selection; $D1$ and $D2p$ correspond to bimodal equilibrium distributions, $D2m$ to unimodal distributions. White area $D1$: distribution described by eqn (11); Light grey and grey areas $D2p$ and $D2m$: distribution given in eqn (8). The thick full black boundary delimiting the S area is given by $Y = 0$ (see eqn 6); the dashed boundary delimiting the $D2m$ area corresponds to $X = 0$ (see eqn 9). The thin dashed line delimiting $D1$ and $D2p$ is $\sigma_R = \sigma_S$. Subfigures (b)–(f) show the equilibrium distributions of traits (black curves) in the clonal model, and the distributions of resources (filled grey curves); their parameters are shown on subfigure (a). $\sigma_R/\sigma_S = 1.15$ in (b)–(d); 0.75 (e), (g); 0.35 (f). $\Delta\theta/\sigma_S = 0.5$ (b), (e); 1.85 (c), (f), 3.75 (d), (g).

I look for the conditions under which species diversity can be maintained by selection (i.e. in the absence of recurrent mutations or migration). The different types only differ in their ecological trait U and reproduce synchronously. Note that this is equivalent to assuming that individuals with different Us belong to the same species but reproduce clonally, or also that individuals are haploid and the trait U is coded by a single locus with a continuum of alleles.

Ecological model
When individuals breed true and selection is on survival only, reproduction does not affect the distribution p of types. I denote the proportion of the population with trait U at time t as $p_t(U)$. The proportion of the

population with trait U at the next generation is the following:

$$p_{t+1}(U) = w(U)p_t(U)$$
$$= \int_{-\infty}^{+\infty} \frac{F(U,x)}{\int_{-\infty}^{+\infty} F(V,x)p_t(V)dV} R(x)dx \, p_t(U) \quad (5)$$

I now look for an equilibrium of model (5) where only one species is present and study its stability against small perturbations. If such an equilibrium is stable, selection is locally stabilizing, and speciation cannot occur with gradual evolution. Technically, finding such a monomorphic equilibrium and studying its stability actually corresponds to identifying singular

strategies and assessing their invadabilities, under an adaptive dynamics framework (Geritz et al., 1998).

Deriving the conditions for disruptive selection
I use an adaptive dynamics approach (Geritz et al., 1998) to determine whether selection is locally stabilizing or disruptive, and I show in section A.3 in Appendix S1 (Supporting Information) another method, which is moment-based, for deriving this result. Selection is called disruptive when the variance of the distribution of phenotypes is larger after the selection step than just before.

The invasion fitness of a mutant individual with foraging trait U_m in a population fixed for the trait U_r (i.e. $p(U_r) = 1$) reads:

$$w(U_m, U_r) = \int_{-\infty}^{+\infty} R(x) \frac{F(U_m, x)}{F(U_r, x)} dx$$

It is the sum over all resources x of the relative resource intake of individuals with trait U_m compared to residents with trait U_r. The corresponding fitness gradient $\delta w(U_r)$ reads, after some algebra:

$$\delta w(U_r) = \left. \frac{\partial w(U_m, U_r)}{\partial U_m} \right|_{U_m = U_r}$$
$$= \frac{\bar{x} - U_r}{\sigma_S^2}$$

and it is straightforward to see that the fitness gradient vanishes ($\delta w(U_r) = 0$) at the intermediate foraging trait $U^* = \bar{x} = q\theta_1 + (1-q)\theta_2$, which is therefore a singular strategy. We have therefore identified a potential equilibrium solution of model (5), p_S^*, in the form of a delta peak at the singular strategy $\bar{x}$, $\delta_{\bar{x}}$ (such a distribution is shown in Fig. 1e,f). We now have to assess the stability of this equilibrium distribution. The singular strategy $U^* = \bar{x}$ can always be reached by gradual evolution (i.e. it is convergence stable, CS, Eshel et al., 1997; Geritz et al., 1998), because:

$$\frac{d\delta w(U_r)}{dU_r} = -\frac{1}{\sigma_S^2} < 0$$

This strategy U^* cannot be invaded by any other strategy (i.e. is an evolutionary stable strategy, ESS), when:

$$\left. \frac{\partial^2 w(U_m, U_r)}{\partial U_m^2} \right|_{U_m = U_r} = \frac{q(1-q)\Delta\theta^2 + (\sigma_R^2 - \sigma_S^2)}{\sigma_S^4} < 0 \quad (6a)$$

with $\Delta\theta = \theta_2 - \theta_1$, and so I define Y:

$$Y = \Delta\theta^2 + \frac{1}{q(1-q)}(\sigma_R^2 - \sigma_S^2) \quad (6b)$$

This means that the equilibrium distribution $p_S^* = \delta_{\bar{x}}$, corresponding to the persistence of only one type $U^* = \bar{x}$, is locally stable when $Y < 0$ (in the

absence of recurrent mutations or migration). In other words, selection is locally stabilizing when $Y < 0$: with gradual evolution, i.e. small mutation steps, speciation can therefore not occur when $Y < 0$. In Fig. 1a, $Y = 0$ is the equation of the full thick black curve. When $\Delta\theta = 0$, $Y < 0$ ensures global evolutionary stability (see section A.2.2 in Appendix S1). When $\Delta\theta > 0$, numerical investigations indicate that $U^* = \bar{x}$ is not always globally evolutionary stable when it is locally evolutionary stable, especially when the distribution of resources is very asymmetrical (low or high q, see the red area in Fig. S4). In these cases, U^* is a local, but not global fitness maximum when $Y < 0$, and alternative equilibria exist. When the resources are symmetrical ($q = 1/2$, the case considered by TPH) however, $Y < 0$ implies global evolutionary stability.

$Y > 0$ is not always a sufficient condition for ecological speciation. First, it may lead to diversification, but not always to the 'disruption' of the population into distinct phenotypic clusters. Characterizing the exact shape of p^* in the next section, we will indeed see that even with our ecological model, the equilibrium distribution of traits may remain unimodal (as already noted by Roughgarden, 1972; Polechová & Barton, 2005; Leimar et al., 2008, in the case of unimodal resource distributions, when $\Delta\theta = 0$). Second, branching in clonal populations does not necessarily translate into speciation in sexually reproducing populations.

Finally, it is interesting to note that Y combines both the intensity of competition (through the width of the foraging ability function, σ_S), and the shape of the global resource distribution: the global variance of the distribution of resources is indeed $q(1-q)\Delta\theta^2 + \sigma_R^2$.

Recovering classical results as limiting cases
Classical results for limiting cases such as strictly unimodal resources, or discrete resources can be recovered.

Unimodal resources: For strictly unimodal resources ($\Delta\theta = 0$), condition (6) tells us that selection is stabilizing when

$$\sigma_R < \sigma_S$$

This setting ($\Delta\theta = 0$) is similar to Roughgarden (1972)'s model, and the above condition is analogous to the condition derived by Dieckmann & Doebeli (1999). Note however that Dieckmann & Doebeli (1999) modelled direct competition (scaled by the σ_C parameter in their study), while in the present model competition is indirect, via the width of the foraging functions (σ_S).

Levene model: For discrete resources ($\sigma_R \to 0$), selection is stabilizing when

$$(\Delta\theta/\sigma_S)^2 < \frac{1}{q(1-q)}$$

which is equivalent to the condition derived in Levene-type models (Kisdi & Geritz, 1999). This condition on the relative distance between resource peaks can be translated in terms of trade-off shapes (Débarre & Gandon, 2010) and has also been derived by Barton (2010).

Equilibrium distribution of traits in the ecological model – conditions for bimodality

I now derive explicit solutions of model (5), and I look for conditions under which these solutions are multimodal, i.e. it is possible to identify different clades or clusters of types. This provides a second axis, X, for reanalysing TPH's data.

Under stabilizing selection (Y < 0)
As explained in the previous section, the equilibrium distribution of traits is a delta peak (i.e. a very narrow peak) at $U = \bar{x}$, the mean resource, when $Y < 0$ (see Fig. 1e,f):

$$p_S^*(U) = \delta_{\bar{x}}(U) \qquad (7)$$

This corresponds to locally stabilizing ecologically based selection, a situation where speciation cannot occur under gradual evolution with this model. We now have to determine what the equilibrium distribution of traits is when p_S^* is unstable, i.e. when $Y > 0$.

Under disruptive selection (Y > 0)
The equilibrium distribution of traits, p^*, is such that for all U, $p_{t+1}^*(U) = p_t^*(U)$, i.e. is such that for all U, either $w(U)=1$ or $p^*(U) = 0$. Its shape depends on the relative values of σ_R and σ_S.

When the resource distributions are wider than the foraging abilities ($\sigma_R > \sigma_S$), it can be shown that the equilibrium distribution of traits is the weighted sum of two Gaussians, each with variance $\sigma_R^2 - \sigma_S^2$:

$$p_{D2}^*(U) = \frac{1}{\sqrt{2\pi(\sigma_R^2 - \sigma_S^2)}} \left[q \exp\left(-\frac{(U-\theta_1)^2}{2(\sigma_R^2 - \sigma_S^2)}\right) \right.$$
$$\left. + (1-q)\exp\left(-\frac{(U-\theta_2)^2}{2(\sigma_R^2 - \sigma_S^2)}\right) \right] \qquad (8)$$

The distribution p_{D2}^* is a solution because for all U, $w(U)$ calculated according to eqn (4) is equal to unity (see section A.4.2 in Appendix S1 for details of the calculations).

The question is then whether this distribution is bimodal or not (compare Fig. 1b–d). In the general case, I could not find a general analytical criterion – the mode can however be numerically determined for

any q, and is plotted as a thick black dashed curve in Fig. 1a, where $q = 1/3$. For the particular case where the resource peaks have the same height ($q = 1/2$), one way to characterize the bimodality is to look at the concavity of the distribution at the trait corresponding to the mean resource, i.e. at $p_{D2}^{*\prime\prime}(\bar{x})$; this concavity at $\bar{x}$ is given by the sign of X, defined as:

$$X = \Delta\theta^2 - 4(\sigma_R^2 - \sigma_S^2) \qquad \text{when } Y > 0 \qquad (9)$$

When selection is locally disruptive ($Y > 0$), the equilibrium distribution is bimodal when $X > 0$. As TPH focused on the case where the resource distribution is symmetrical ($q = 1/2$), this defines our second axis, X, when reanalysing TPH's data. This condition means that the resources have to appear bimodal at the scale of the width of the foraging abilities σ_S: the term $\Delta\theta^2 - 4\sigma_R^2$ is indeed the concavity at the mean resource $\bar{x}$ of the distribution of resources when $q = 1/2$. X is an increasing function of σ_S, the width of the foraging ability function. As discussed in models of unimodal distributions of resources ($\Delta\theta = 0$) (Roughgarden, 1979), a larger σ_S makes competition for resources stronger and leads to the competitive exclusion of too similar types; hence, with a higher σ_S, each peak of the equilibrium distribution of phenotypes is narrower, and the distribution is more likely to look bimodal. Note that with TPH's original *shape* parameter ($shape = \exp[-\Delta\theta^2/(2\sigma_R^2)]$), unimodal distributions could be (erroneously) described as bimodal (see Fig. S1b). As the equilibrium distribution is unimodal when selection is stabilizing ($Y < 0$), we can arbitrarily set $X = -1$ when $Y < 0$. When $q = 1/2$, conditions (6) and (9) can be combined in a single axis, χ, so that selection is locally disruptive and the equilibrium distributions are bimodal when:

$$\chi = \Delta\theta^2 - 4|\sigma_R^2 - \sigma_S^2| > 0 \qquad (10)$$

where the notation $|x|$ refers to the absolute value of x.

When the foraging abilities are wider than the resource distributions ($\sigma_R \leq \sigma_S$), the Gaussians of p_{D2}^* concentrate into delta peaks (see e.g. Doebeli *et al.*, 2007, for the $\Delta\theta = 0$ case, and section A.4 in Appendix S1), so that the equilibrium distribution is:

$$p_{D1}^*(U) = q\delta_{\theta_1}(U) + (1-q)\delta_{\theta_2}(U) \qquad (11)$$

and the distribution is always bimodal when $\theta_1 \neq \theta_2$, i.e. $\Delta\theta \neq 0$ (which yields $X > 0$). This corresponds to the $D1$ area in Fig. 1a and to a distribution such as the one drawn on Fig. 1g.

The conditions $Y > 0$ and $X > 0$ are necessary for the distribution of types coexisting at equilibrium to be bimodal, in this ecological model where all functions are Gaussian or sums of Gaussians, and when evolution proceeds gradually. As emphasized earlier, this does not

ensure that speciation will occur. However, with gradual evolution, ecological speciation will not occur in the fully sexual model if $Y < 0$; but also, even when $Y > 0$, we will not be able to identify as different species two too similar clades when $X < 0$.

I now go back to a model with sexual reproduction, and identify a third axis to reanalyse TPH's data.

Strength of assortment

Measuring the strength of assortment

The effect of the strength of assortment cannot be evaluated with my ecological model (5). While analytical insights can be gained with an infinitesimal sexual model in the limit case where $\Delta\theta = 0$ (Polechová & Barton, 2005), calculations are much more complicated in the general case where $\Delta\theta \neq 0$. I therefore rely on TPH's simulations to assess the effect of the strength of assortment.

Thibert-Plante & Hendry (2011) included in their simulations potential for premating isolation, by allowing for assortative mating based on the ecological trait U (i.e. assortment based on a 'magic' trait). A parameter c measures whether mating is assortative ($c > 1/2$), random ($c = 1/2$) or disassortative ($c < 1/2$), and another parameter, σ_A, measures the width of the preference function Ψ. In TPH's simulations, all individuals are hermaphrodites, and all individuals (as females) mate and produce offsprings. All individuals can also be chosen as potential fathers; encounters are random, and a female f accepts at male with trait m with a probability scaled by $\Psi(f,m,c)$. In Thibert-Plante & Hendry (2011), this preference function reads:

$$\Psi(f,m,c) = \begin{cases} \exp\left[-(2c-1)^2 \frac{(f-m)^2}{2\sigma_A^2}\right] & c > 1/2 \\ 1 & c = 1/2 \\ \exp\left[-(2c-1)^2 \frac{(f-(1-m))^2}{2\sigma_A^2}\right] & c < 1/2 \end{cases}$$

To measure the intensity of assortative mating, I use (almost) the same compound parameter as TPH's *sdSex*: I define

$$Z = (2c-1)^2/(2\sigma_A^2) = 1/(2\,sdSex^2) \qquad (12)$$

Mating is random when $Z = 0$, and there is some assortative mating when $Z > 0$, its strength increasing with Z. I use the squared inverse of TPH's *sdSex* to prevent infinite values of the index for random mating. This index cannot account for disassortative mating (Z is always positive), which is however not problematic because I have removed from my analysis data corresponding to $c < 1/2$.

An alternative function for assortative mating

I did remove simulation results with $c < 1/2$, because the function Ψ described in Thibert-Plante & Hendry (2011) does not always lead to disassortative mating

when $c < 1/2$ (see Fig. 2a). A female $f = 0$ will preferentially mate with a male $m = 1$, which is the most different type. However, a female $f = 1/2$ will mate preferentially with a male $m = 1/2$: there is assortative mating in spite of $c < 1/2$. This function Ψ was introduced by Gavrilets *et al.* (2007) to correct the 'artifactual strong disruptive selection' in the mating preference functions used by, e.g. Doebeli (2005) or Bolnick (2006) (see Fig. 2b), but I show here that this function does not accurately represent disassortment. An alternative function, which would still model disassortment and not produce artificial disruptive selection could look like this (see Fig. 2c):

$$\Phi(f,m,c) = \begin{cases} 1 - (2c-1)^2\left[1 - \exp\left(-\frac{(f-m)^2}{2\sigma_A^2}\right)\right] & c > 1/2 \\ 1 & c = 1/2 \\ 1 - (2c-1)^2\left[\exp\left(-\frac{(f-m)^2}{2\sigma_A^2}\right)\right] & c < 1/2 \end{cases}$$

$$(13)$$

These different preference functions are illustrated in Fig. 2. One advantage of the function I suggest (eqn 13) is that it teases apart the strength of the choice, c, from the width of the preference function, σ_A. Mathematically speaking, the fact that Φ is continuous and differentiable in c is also a good point [and using fourth powers $(2c-1)^4$ instead of squares would even make Φ twice differentiable in c, which can be convenient for analysis].
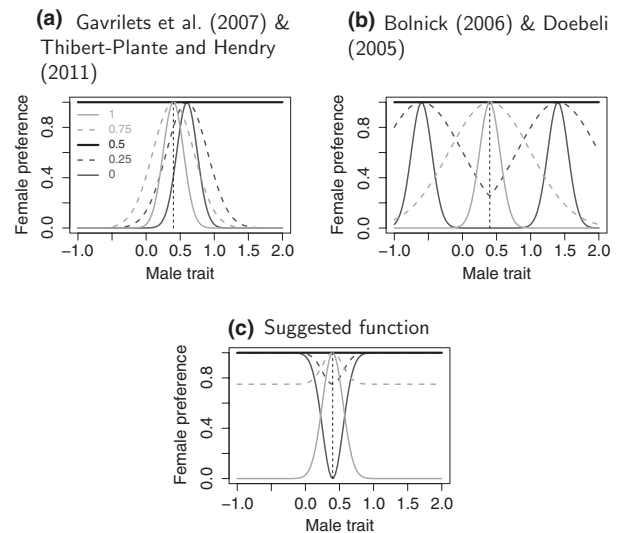
Fig. 2 Different preference functions: Strength of preference of a female $f = 0.4$, for different males (x-axis), and different values of c [Legend in (a)]. (a) the function used in Thibert-Plante & Hendry (2011), which does not lead to disassortment when $c < 1/2$. (b) another function, which leads to strong disruptive selection when $c < 1/2$. (c) a suggested alternative function, see eqn (13).

Comparing the analytical conditions for speciation to TPH's results

Xavier Thibert-Plante kindly provided their simulation results. I analysed them with R (R Development Core Team, 2010) and used the packages multicore (Urbanek, 2011, for parallel computing), R.basic (Bengtsson, 2011, for 3d plots) and plotrix (Lemon, 2006, for pie charts). The analysis of the ecological model was performed with the help of Mathematica 7 (Wolfram Research).[1]

I removed from TPH's dataset data where $\sigma_S = 1000$ or $\sigma_R = 1000$, because these correspond to virtually no selection, introducing noise into our conclusions regarding which factors promote sympatric speciation.

I use TPH's criterion for sympatric speciation, that is, whether there are fewer hybrids than expected in the absence of selection (see Thibert-Plante & Hendry, 2011, for more details), because this is the piece of information on the distribution of phenotypes which is saved in their simulation results. Keeping TPH's notations, I identify zones corresponding to full sympatric speciation (0, when there are no hybrids), progress towards sympatric speciation (1) and no sympatric speciation (2). TPH's criteria for distinguishing between the (1) and (2) zones relying on quite arbitrary values, I chose a slightly more stringent condition for a simulation to be classified as in the (1) zone instead of (2) (i.e. a proportion of individuals with an intermediate phenotype representing < 40% of the proportion without selection nor mate choice, instead of 60% in TPH's study).

I removed from the analysis data corresponding to zone (3): no sympatric speciation and failure to adapt. Data points in zone (3) may correspond to unfinished simulations [because 3000 generations is maybe not enough to reach equilibrium (S. Yeaman, personal communication)], but also to numerical artifacts due to extremely small numbers being rounded to 0 (see Discussion). With TPH's boundaries for the four zones, data in the (3) zone represented about 6% of the total simulations.

I show in Fig. 3a the proportion of TPH's simulations where full sympatric speciation and progress towards sympatric speciation [zone (0) and (1), respectively, with TPH's notations] were recorded (black and dark grey areas in the pie charts, respectively), as a function of the three criteria identified earlier: whether the relative mode of the distribution of resources is uni- or bimodal (X-axis, eqn 9), whether selection is locally stabilizing or disruptive (Y-axis, eqn 6), and whether mating is random or not (Z-axis, eqn 12). Note that by definition, X can only be positive if Y is positive, which is why there are no pie charts on the front edge of the cube. With these three axes, two of them being new compared to

TPH's analysis, we clearly see that sympatric ecological speciation occurs *in this model* where all functions are Gaussian or sums of Gaussians, with at the same time locally disruptive ecologically based selection (Y axis), resources which are differentiated enough (X axis), and non random mating (Z axis); all conditions are met at the back top-right vertex of the cube in Fig. 3a. Figure 3b shows the detail of the interaction between χ (which combines X and Y) and Z. We see that sympatric ecological speciation is favoured when mating is more assortative (higher Z), and selection more locally disruptive and resources different enough ($\chi > 0$). Note that a very small number of simulations are recorded as having led to full sympatric speciation, while their parameters correspond to $\chi < 0$. Finally, the details of each axis, independently of the others, are presented in Fig. S3.

TPH's model contained a few complications which I neglected in this study; in particular, while I assumed that survival probabilities were directly proportional to fitness, TPH introduced non linearities. Although this may affect the dynamics of the system, we see that the conditions I derived with a simpler model are robust (Fig. 3).

Discussion

Conditions for sympatric diversification

In this article, I investigate the conditions for sympatric ecological speciation by analysing a model inspired by a recently published study (Thibert-Plante & Hendry, 2011, henceforth TPH). I first focus on an ecological model of species coexistence and I derive necessary conditions for the equilibrium distribution of types to be multimodal. I show that the shape of this equilibrium distribution depends on whether selection is locally disruptive (i.e. whether more than only one type persists at equilibrium or, equivalently here, whether the variance of the distribution of phenotypes can be larger after selection than before), but also on whether resources are enough differentiated. I then test and confirm these conditions against TPH's data. The analytical insights gained from the analysis of the clonal model help better understand the results of TPH's simulations.

The role of (absolute) resource bimodality
My analysis shows that what matters for sympatric speciation is not the absolute bimodality in resources (given by $\Delta\theta^2 - 4\sigma_R^2 > 0$ when $q=1/2$), but a *relative* bimodality, scaled relative to σ_S, the width of the foraging function F (see eqn 9). In the ecological model, multimodal equilibrium distributions can hence also occur with absolute unimodal resources (as illustrated in Fig. 1c).

TPH found in their data some (rare) occurrences of sympatric speciation with (absolute) unimodal

(a) Three factors for ecological speciation   **(b)** Detail of the interactions
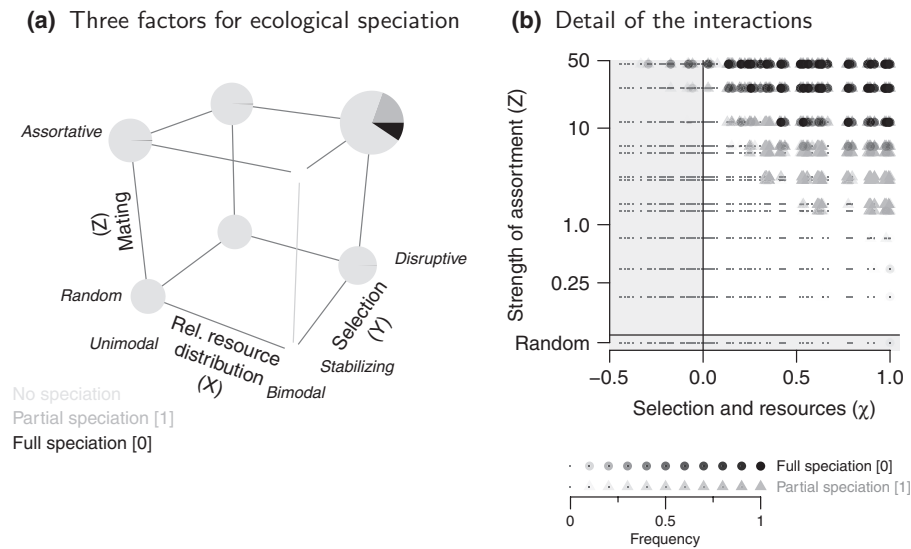

Fig. 3 Checking the conditions for sympatric speciation with Thibert-Plante & Hendry (2011) data. (a) The data are divided according to three axes: whether the relative mode of the distribution of resources is unimodal or bimodal (X, see eqn 9), whether selection is locally stabilizing or disruptive (Y, eqn 6), and whether mating is at random or there is some assortment (Z, eqn 12). The black (resp. dark grey) areas in the pie charts show the proportions of the simulations where full sympatric speciation (resp. progress towards sympatric speciation) happens [zones (0) and (1) in TPH]; the size of each pie chart indicates the number of parameter combinations satisfying the conditions corresponding to each vertex. (b) Detail of the interactions. The horizontal axis is χ (see eqn 10), which combines X and Y; the vertical axis is the strength of assortment Z. All combinations of parameters are plotted; for each combination, the symbol indicates the proportion of simulations where there is progress towards sympatric speciation (grey triangles) or full speciation (black dots) (legend below the plot).

resources, which is quite surprising given that their criterion for (absolute) unimodality is much more stringent than mine (i.e. they call bimodal distributions which are in fact unimodal, see Fig. S1b). However, their dataset includes simulations run with virtually no selection ($\sigma_S = 1000$ or $\sigma_R = 1000$ correspond to flat curves given the $(-1,1)$ range of possible phenotypes), in which evolution occurs much more slowly – after 3000 generations with these parameters, only drift may have acted and changed the distributions of traits. Interestingly, the majority of cases where full sympatric speciation with unimodal distributions was recorded by TPH corresponds to these no selection simulations (see grey dots on Fig. S2, to be compared to the black dots, where the no selection data have been removed). Hence, TPH's data tend to suggest that sympatric ecological speciation does require (absolute) bimodal resources (with well-mixed, unstructured sexual populations). Whether this finding will hold when simulations are run for longer (e.g. greater than 3000 generations) or when assortment is stronger (e.g. $c \rightarrow 1$), or when non Gaussian functions are used (Sasaki, 1997; Gyllenberg & Meszena, 2005), but also, and maybe mainly, with more 'flexible' genetic architectures, will require further investigations. With (absolute) unimodal resources indeed, other studies have already found diversification (Doebeli *et al.*, 2007;

Zhang & Hill, 2007; Pigolotti *et al.*, 2010), or the maintenance of ecologically equivalent types (provided a spatial heterogeneity in resource availability, M'Gonigle *et al.*, 2012), as well as the evolution of more assortative mating (de Cara *et al.*, 2008; Pennings *et al.*, 2008).

Hard selection, soft selection and frequency dependence

The model studied in the present article is highly frequency-dependent: the relative share of individuals with trait U on a resource x depends on the *relative* foraging efficiency $\omega(U,x)$ of those individuals on this resource, no matter if their absolute foraging efficiency $F(U,x)$ is extremely low. This may in some instances look unrealistic, but this explicit model is behind the widely used competition functions for limiting similarity (Ackermann & Doebeli, 2004). Incidentally, this may also explain why TPH observed for some parameters in their simulations adaptation to a single peak of resources [zone (3) in their results], a result which should never occur according to the ecological model, because the singular strategy $\bar{x}$ is always convergence stable. This convergence stability is due to the fact that mutants may have a better, although extremely low in absolute terms, foraging ability than the resident population on the distant resource peak, which results in a

better fitness, and allows the mutants to invade. In numerical simulations, there is a lower limit in real numbers; a very low $F(U',x')$ may be set equal to zero, so that $\omega(U',x')$ will also be equal to zero, while, in the analysis, $\omega(U',x')$ will be positive. Hence, if in the simulations the population first drifts towards one resource peak only, it may be trapped there, and not be able to adapt to the other resource peak.

Thibert-Plante & Hendry (2011) allowed for demographical dynamics – population densities were not fixed in their simulations – and the output from each resource could therefore vary. However, and contrary to their claim, their model remain closer to soft selection than hard selection. It is closer to soft selection because of the strong frequency dependence (Christiansen, 1975; Débarre & Gandon, 2011), which is also highlighted by the fact that the equations of a Levene-type model are recovered when $\sigma_R = 0$ (Kisdi & Geritz, 1999; Kisdi, 2001). In addition, soft selection promotes polymorphism, while sympatric speciation would not be possible in a 'real' hard selection model, where fitness would not be frequency-dependent on each resource. Under hard selection, model (5) would read:

$$
\begin{aligned}
p(U)^{(t+1)} &= W(U)p(U)^{(t)} \\
&= \frac{\int_{-\infty}^{+\infty} F(U,x)R(x)\mathrm{d}x}{\int \int_{-\infty}^{+\infty} F(V,x)R(x)p(V)^{(t)}\mathrm{d}V\mathrm{d}x}p(U)^{(t)}
\end{aligned} \quad (14)
$$

It can be shown that in model (14), the equilibrium distribution of traits is always unimodal, and therefore that sympatric speciation is impossible. Hence, sympatric speciation requires some level of frequency dependence on resource acquisition.

Conclusion

To conclude, my reanalysis of TPH's model confirms that in well-mixed populations, with spatially and temporally constant selection, quantitative traits determined by multiple additive loci, where individuals are identified according to their ecological trait only (e.g. in the absence of ornaments involved in sexual selection), sympatric ecological speciation is favoured when: selection is locally disruptive (Y, eqn 6), resources are heterogeneous enough (X, eqn 9), and, for sexual reproduction, mating does not occur at random (Z, eqn 12).

The genetic architecture chosen by Thibert-Plante & Hendry (2011) was very constrained and may have limited the potential for speciation even when the three conditions I identified ($X > 0$ and $Y > 0$ and $Z > 0$) were met. Further developments could investigate whether less constrained genetic architectures (i.e. continuum of alleles at each locus instead of –/0/+ alleles), or even evolvable architectures (Yeaman & Whitlock, 2011) make sympatric ecological speciation easier or not.

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Supporting information

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

Appendix S1 Printouts of the Mathematica and R scripts deposited at Dryad.

Figure S1 Distributions of the types of resources and their modes, for different values of the $\Delta\theta/\sigma_R$ ratio.

Figure S2 Frequency of full sympatric speciation in TPH's simulations with or without no-selection data.

Figure S3 Decomposition of TPH's results along the X, Y and Z axes independently.

Figure S4 Assessing the global stability of the singular strategy $\bar{x}$, for different values of $\Delta\theta$ (101 points, $0 < \Delta\theta < 10$; horizontal axis), q (101 points, $0 < q < 1$; vertical axis), and σ_R (101 points, $0\,\sigma_R\,\sigma_S$).

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