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Agent-based models of competitive speciation I: effects of mate search tactics and ecological conditions

Rainer Hilscher

Informatics Department, Evolutionary and Adaptive Systems Group,
University of Sussex, Falmer, Brighton BN1 9RH, UK

ABSTRACT

Aims: To understand competitive speciation dynamics of an initially monomorphic and randomly mating population under different ecological conditions (different food resource distributions) and different competition scenarios (competition between specialist, intermediate and generalist individuals). To compare the speciation potential of two female mate-search tactics (best-of-*n* and threshold).

Model: Generational agent- (or individual-) based simulation model with male and female individuals; polygynous mating system with explicit leks and two different female mate-search tactics; explicit modelling of food resource; explicit implementation of an ecological range variable (a_{eco}) determining the range of food objects individuals of a given phenotype can eat (and thus the competition between individuals).

Key variables: Individuals in one-trait experiments are characterized by a phenotype consisting of two traits, T_{eco} (defines preferred mates for females and preferred food objects for all individuals) and $T_{mate\text{-}range}$ (defines the degree of assortative mating of females). In two-trait experiments, females select mates according to T_{mate} (a mating trait independent of T_{eco}).

Conclusions: Given a one-trait system, a population can undergo competitive speciation to completion. New species occupy niches located anywhere in the environment and not just in the extreme regions; species constellations are determined by (a_{eco}). Given a spatially explicit ecological gradient model, populations do not speciate in geographical space; thus neighbouring individuals constantly compete. Best-of-*n* mating usually promotes speciation better than threshold mating. Speciation may also occur in a two-trait system, although in such a case assortative mating has to evolve also. Such speciation depends on a more restricted set of parameter values than does the one-trait case.

Keywords: agent-based model, assortative mating, competition, individual-based model, mating strategy, niche width, sympatric speciation.

INTRODUCTION

Darwin saw the generation of new species mainly as the product of competitive interactions for a limited resource. His ‘selectionist’ perspective of speciation lay dormant for much of

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* e-mail: rainerh@sussex.ac.uk

the last century, completely dominated by a focus on geography as the main cause of speciation (see Schilthuizen, 2001). Competition as a mature agent of diversification was reintroduced by Rosenzweig in 1978 with a landmark paper on 'competitive speciation' (Rosenzweig, 1978). Several other papers were published subsequently (Gibbons, 1979; Seger, 1985) but it was Doebeli's quantitative genetic model of competitive speciation (Doebeli, 1996) that initiated the recent emphasis on this kind of model set-up in the form of adaptive dynamics. Adaptive dynamics (Dieckmann, 1997; Geritz *et al.*, 1998; Dieckmann and Metz, 2001) presents the most sophisticated mathematical framework that has been successfully applied to the problem of sympatric speciation. [For a critical review of adaptive dynamics, see Waxman and Gavrilets (2005).]

In its most basic form, adaptive ecological speciation posits that an optimally adapted mean phenotype (such as beak size) of a population inhabiting an environment with a continuous distribution of a limited resource, such as food, might actually represent a fitness minimum because 'optimal' individuals experience more selection pressure through competition. Mutant individuals with more extreme phenotypes located on either side of the distribution will have higher fitness due to reduced competition and are thus able to invade the population. If the width of the food resource distribution is wider than the width of the distribution of competition between individuals, adaptive branching will occur with the end result of two, reproductively isolated species occupying the two extreme regions of the resource distribution.

Several published models of ecological speciation have explored many aspects of ecological speciation (Dieckmann and Doebeli, 1999; Drossel and McKane, 2000; Doebeli and Dieckmann, 2003; Bolnick, 2004). The basic set-up includes a unimodal distribution of a food resource and competition for this resource described by a continuous form of the Lotka-Volterra equations with a given competition parameter as a function of the phenotypic distance between two individuals. Competition is stronger between individuals of similar phenotype than between phenotypically distant individuals. Space is not explicitly modelled. This basic set-up is used by Drossel and McKane (2000) in a quantitative genetic model of competitive speciation that does not belong to the adaptive dynamics class of models. Their model considers a 'no-gene' (Coyne and Orr, 2004) or magic trait (Gavrilets, 2004) solution where the ecological and the assortative mating trait are the same and assortative mating is assumed from the start. Dieckmann and Doebeli (1999) and Doebeli and Dieckmann (2003) present individual-oriented individual-based models [as opposed to 'true', narrowly defined individual-based models (Uchmański and Grimm, 1996)] of ecological speciation from the perspective of adaptive speciation. These authors consider both a magic trait and a two-trait (the ecological and assortative mating trait are different) scenario and assortative mating is treated as an evolvable trait. Speciation occurs in both scenarios. Bolnick (2004) extends the basic model of Dieckmann and Doebeli (1999) by manipulating the strength of assortative mating. Compared with the strong assortative mating assumed by the Dieckmann and Doebeli models, Bolnick finds that with weaker assortative mating, waiting time to speciation increases significantly, in particular in the two-trait model.

A further extension of the basic model includes an explicit implementation of space (Doebeli and Dieckmann, 2003). If individuals evolve along an ecological gradient, Doebeli and Dieckmann (2003) find that speciation occurs under a wider range of parameter settings than in the non-spatial model. For the remainder of this paper, the above models by Dieckmann and Doebeli will be referred to as D&D models.

PREMATING ISOLATION

Given the prominent role premating isolation plays in sympatric speciation, one would expect to find various implementations of mate search tactics and detailed analysis of the effect of different mate search behaviours. Intriguingly, the ecological speciation modelling landscape presents itself pretty much as a flat plain regarding mate search tactics. Some form of affinity best-of-*n* (Arnegard and Kondrashov, 2004), where females pick the closest male to their own ecological or mating-preference phenotype, is the *de facto* standard.

Disruptive selection and mate choice can operate on different genetic architectures. On a very basic level, a distinction can be made between loci that code for the trait (or traits) that is (are) the target of disruptive selection and loci that code for the trait (or traits) that is (are) the target of mate choice. Both sets of loci may be the same, in which case the same trait is disruptively and sexually selected. This constellation is commonly assumed to be the easiest for sympatric speciation to occur and is synonymously referred to as a one-trait system (Fry, 2003), a single-variation system (Rice and Hostert, 1993) or as a magic trait system (Gavrilets, 2004). A system with different disruptively selected and mate choice traits is referred to as a two-trait (Fry, 2003) or double-variation system (Rice and Hostert, 1993). Two-trait genetic systems provide a less favourable genetic architecture for speciation than one-trait systems because a genetic correlation between genes coding for the premating isolation trait and those genes coding for the trait under disruptive selection has to evolve.

Mate search tactic

What search tactics females employ in finding mates in an asymmetric mating system where only females choose and males compete is still a contested issue in sexual selection research (Gibson and Langen, 1996). Two basic search tactics feature prominently in empirical and theoretical research (Wiegmann *et al.*, 1996, 1999): (1) best-of-*n* search where the successful male is the best one out of a competing set of *n* males, and (2) threshold (or sequential) search where a female accepts any male that exceeds a certain quality value. Sequential search may significantly reduce the cost of mate selection because a female can terminate her search once a suitable male has been encountered.

These two search tactics define two implementations of either assortative or preference mating with a direct influence on the evolution of premating isolation. Threshold, or sequential, search offers the more intuitive and less controversial alternative. A female may abandon her search for a mate relatively quickly once she has encountered a suitable male that exceeds her personal acceptance threshold value. The first male whose phenotypic distance falls above the female's acceptance threshold will be chosen as her mate (resulting in positive assortative mating). Premating reproductive isolation is easily envisioned in a model given threshold search. The threshold value is implemented as an evolvable trait and initialized to a relatively high value (for details, see below) effectively resulting in random mating. Reproductive isolation has evolved once the threshold has decreased to a value where females of one eco morph refuse any male as mates from the other eco morph.

With best-of-*n* search, we are confronted with a theoretical conundrum regarding the biological status of species. Again, imagine the simplest case of phenotypic distance. Given best-of-*n* search, a female selects the male who is closest to her own phenotype (given positive assortative mating). If a female encounters a lek of males consisting of males from her own ecological cluster and from the other cluster (assuming a population has split into two) she will pick one of her own kind, specifically the closest of her male compatriots. Similarly, if she is confronted with a lek of males composed solely of males from the other cluster she will again pick the closest male. This would violate the complete premating isolation requirement of traditional interpretations of the biological species concept (BSC) because gene flow would exist. To speak of speciation in the context of best-of-*n* search, one thus has to relax the complete reproductive isolation requirement for successful speciation. Otherwise, it would not be speciation that has occurred but 'only' the evolution of a resource polymorphism (Skúlason and Smith, 1995). More recent revised interpretations of the BSC (Noor, 2002; Coyne and Orr, 2004) accept a low level of gene flow which would solve the theoretical best-of-*n* conundrum.

In this paper, polymorphism refers to an unstructured continuous population distribution and resource polymorphism to a structured population distribution with distinct phenotypic clusters that are not reproductively isolated due to high levels of gene flow (Skúlason and Smith, 1995). Speciation is assumed once near complete reproductive isolation has evolved in correspondence with the revised BSC.

Goals of this study

This study addresses two sets of problems by running agent-based models (ABMs; agent-based models are related to but are more sophisticated than individual-based models; ABMs are commonly used in artificial life or computational economics and sociology contexts). The first problem relates to the almost completely overlooked question in speciation studies of how females choose their mates and in how far this choice of mate search tactics affects speciation dynamics (but see Kawata, 2001). Assortative mating plays an integral role in ecological sympatric speciation but has been mainly neglected as a research target. The present study compares the performance of two search tactics, best-of-*n* and threshold, in two ecological conditions and several different competitive overlap scenarios. It is found that in the non-spatial, unimodal food distribution scenario the best-of-*n* search tactic is significantly more conducive to speciation than the threshold rule. No such dramatically different performance is evident in the gradient scenario. Speciation dynamics now show fairly similar patterns. This finding confirms Doebeli and Dieckmann's (2003) result that speciation in the gradient ecological scenario occurs under a wider range of parameter settings.

The second problem area relates to model-specific issues of the individual-oriented D&D models [for a detailed description of their spatial model, see Doebeli and Dieckmann (2004, box 7.1)]. An assumed high degree of initial genetic variance in a crucial trait [e.g. maximum variance in mating preference in Dieckmann and Doebeli (1999), Doebeli and Dieckmann (2003) and Bolnick (2004)] is considered a promoting factor in achieving speciation (Waxman and Gavrilets, 2005). In contrast to the aforementioned studies, the simulations presented here were all run with a completely monomorphic population in all traits. This requires a continuous distribution of '1' alleles (given a bi-allelic, additive genetic encoding system) in the founding population of an individual or agent-based simulation (for more details, see 'Detailed model description' section below). Additional runs were produced to test for the effect of initial variance but did not produce qualitatively different results. A related issue is the initial spatial distribution of individuals in the gradient D&D model (Doebeli and Dieckmann, 2003, 2004). Locations of individuals are chosen randomly resulting in a well spread out founding population with a maximum spatial variance. This again should provide a favourable set-up for speciation. [For a detailed description of the spatial D&D model, see Doebeli and Dieckmann (2004, box 7.1).]

Speciation in both D&D models results in a single two-cluster system with an 'uninhabited' central region of the food resource. Sequential speciation events are acknowledged by D&D, albeit in a rather passing manner. In the legend to figure 3 in their 2003 paper (Doebeli and Dieckmann, 2003), a note states that multiple branching events are possible for very small movement distances. This indicates that multiple branching events in their model require a spatially explicit food distribution. A subsection in the epilogue to 'Adaptive speciation' (Dieckmann *et al.*, 2004) also addresses the possibility of sequential branching events. In my model, multiple speciation events occur in both the non-spatial and the spatial food distribution.

Coyne and Orr (2004) speculate whether the possible evolution of a population of 'central' citizens would result in a 'speciation black hole' with the disintegration of the original two-cluster structure into a polymorphism. The results presented in this paper, however, indicate that anything between a strong polymorphism and multiple clusters spread out evenly over the resource distribution is possible. These results indicate a strong model dependency of speciation outcomes. Of particular interest is the way competition is implemented in D&D (1999, 2003) and my ABM model. In my model, competition between individuals is determined by the range of food objects an individual of a given phenotype can eat (e.g. specialist versus generalist feeding strategy). A small range value (specialist individuals) localizes competition in phenotype space and thus implicitly partitions resource space independent of the actual distribution of the resource. D&D models (1999, 2003) do not feature an explicit ecological range variable and instead operate with two independent functions for inter-individual competition and carrying capacity of the environment. They report adaptive speciation resulting in a bi-cluster constellation if the width of the competition distribution function (σ_c) is smaller than that of the carrying capacity (σ_K) but they do not investigate in detail the effect of increasingly smaller values for σ_c on speciation dynamics. Ackermann and Doebeli (2004), in a study with an encoding scheme similar to mine, however, do observe multiple branching events with a cost-induced specialist population (corresponding to a small σ_c).

Other issues with the D&D models include a 'mating equality' effect where females enjoy the same mating success independent of the frequency of their phenotypes (Waxman and Gavrilets, 2005). Rare females have the same probability of finding a mate as common females. This effect is also addressed in this paper. Finally, Waxman and Gavrilets (2005) point out that D&D models share an unrealistically high mutation rate, which in effect churns out a constant higher than natural degree of genetic variation. Similar to the artificial high degree of initial genetic variation, this high constant rate of variance production is thought to facilitate speciation.

In addition to the above contentious issues, this study also addresses the question whether sympatric speciation occurs with the less favourable (to population divergence) two-trait architecture. Speciation did not occur at all in my model with either search tactic and only a modifier implementation of the disruptive best-of-*n* (as defined in Arnegard and Kondrashov, 2004) search tactic produced population divergence. Together these results indicate that ecological sympatric speciation in my model is possible but only under fairly restrictive parameter values and strict assortative mating.

In summary, results show that: (1) competition and assortative mating are responsible for speciation; (2) best-of-*n* mating is much more effective in driving population divergence[1] than threshold mating; (3) monomorphic populations can undergo sympatric speciation to completion; and (4) clustering may also occur in the centre of the food distribution depending on the actual value of competitive overlap. Further results are reported that address other issues of sympatric speciation. Here it is shown that (1) speciation does not occur in geographical space in a spatially explicit model (only in phenotype space) and (2) maximum lek size (females select mates from the entire male population) has a detrimental effect on speciation.

MODEL OVERVIEW – WHY USE AN AGENT-BASED MODEL?

Speciation defines one of nature's most complex large-scale playing fields. Theoretical studies have thus to deal with a trade-off between capturing the essentials of population divergence and keeping simulations simple and tractable. Individual- or agent-based models provide a particularly suitable modelling methodology, since they are able to produce stochastic events that are solely due to the interaction of explicitly implemented individuals and interactions between individuals and their environment. Due to the bottom-up approach of individual-based models, population-wide patterns emerge as the result of interactions of individuals 'living' according to simple rules. Top-down assumptions such as a constant selection pressure independent of population distribution, as in Kondrashov and Kondrashov (1999), are not necessary. [For a short introduction to individual-based models (IBMs) see Judson (1994), for a detailed review of IBMs see Grimm (1999) and for a more technical perspective on IBMs see Berec (2002).] A related model to the one presented here is that of Sadedin and Littlejohn (2003).

Here I present an agent-based model (ABM) that allows a 'plug-and-simulate' approach to performing simulations. Simulation components, or objects, such as different implementations of mate search tactics and ecological scenarios can simply be swapped, since they have to adhere to a predefined 'mate search' or 'ecological scenario' template. The result is a highly versatile platform written in Java[2] that allows running a whole range of different speciation scenarios without compromising inter-simulation result integrity. Theoretical speciation research is hampered by the existence of several fairly different modelling systems rendering the comparison of results almost impossible. A plug-and-simulate computational platform such as the one presented here rectifies this situation, since the underlying parameter assumptions do not change from one simulation to another.

To ensure that the results obtained in the present study can be compared with those of related studies, the model implemented here follows the lead of other individual-based models (Dieckmann and Doebeli, 1999; Doebeli and Dieckmann, 2003; Ackermann and Doebeli, 2004), in particular regarding the use of an explicit genetic system and the implemented magic-trait and two-trait genetic architectures. One major implementation difference to the D&D models is the use of an explicitly implemented food resource. In his study of a two-patch sympatric model, Kawata (2001) uses a similar food implementation scheme. Another very important

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[1] A third, hybrid, mate search tactic where females switch to best-of-*n* mating if they fail to find a mate with the default threshold tactic has been found to be even more effective (Hilscher, 2005).

[2] The actual Java code of the Plug'n Simulate platform can be obtained from http://www.informatics.sussex.ac.uk/users/rainerh/

distinct feature of the present model is the more realistic mating system where females are only presented with a lek of *n* randomly chosen males. In the ecological gradient model, only those males that are spatially close may enter a given lek. Rare females in D&D models enjoy the same mating success as common females. No such modelling skewing measure exists in the lek structure implemented in this study. Parameter effects found in this study (e.g. influence of competitive overlap between individuals on speciation occurrence) correspond to those of Dieckmann and Doebeli (1999) and Doebeli and Dieckmann (2003).

DETAILED MODEL DESCRIPTION

The generational (only offspring make it into the next generation) agent-based model presented here consists of an environment with an explicit food resource and a population of explicitly modelled males and females that compete for this resource (see Table 1 for key assumptions of the model). Individuals have to feed in stage one and only those individuals who succeed in obtaining food will proceed to the mating stage. To avoid any order bias during the feeding stage, individuals (both males and females) are chosen randomly from the entire remaining population to search for food. Once that individual has found an appropriate food object it is removed from the feeding-stage population and added to the mating-stage population. Feeding is controlled by the simple two-step rule 'find a food object close to your location that is close to your phenotype' (this rule is explained in more detail below). This food object is then removed from the environment. The initial number of food objects ($n = 600$) in an environment determines the maximum number of individuals that this environment can sustain. The environment is then reinstated every generation.

A lek of males is produced in the mating stage for a randomly chosen female by randomly picking males from either the entire male population (in non-spatial models) or from the pool of geographically close males (in spatially explicit models). That female then selects a male out of her lek as her mate based on the implemented preference function (threshold or best-of-*n* class of search tactics). Once that female has decided on a male she is taken out of the mating pool. Males may be chosen several times as mating partners resulting in a polygynous mating system. Once all females have selected a male, offspring for the next generation are produced. Each male–female pairing produces three offspring. Additional runs were performed with the number of offspring drawn from a Gaussian distribution, but the results did not differ from those obtained with a fixed number of offspring. Thus, all results presented here were produced with the simpler, fixed-offspring number model variant. Offspring genotypes are the product of sexual reproduction between their parent

Table 1. Key assumptions of ABM model

- discrete generations (consisting only of offspring)
- male and female agents (50 : 50 sex ratio)
- monomorphic initial population in all traits
- polygynous mating with lek
- explicit modelling of food resource
- explicit implementation of an ecological range variable determining (1) the range of food objects individuals of a given phenotype can eat and (2) the competition between individuals
- initial population clustered in middle of ecological gradient (no initial spatial variance)
- every generation is embedded in the exact same ecological setup

genotypes with free recombination of alleles. No pleiotropic effects exist between genes. An offspring has a 50% chance of being male or female resulting in an effective sex ratio of 50 : 50 per simulation.

Mobility m defines the geographical area around agents' location (L_{indiv}) they can scour for food and mates and is fixed for all individuals at 20 units (i.e. 1/6 of the environment's length). Spatial movement of individuals occurs during the feeding stage in the spatially explicit gradient model. It is implemented as a single change of location away from an individual's birthplace to the location where it found an appropriate food object. The maximum distance an individual can move is m. This change of location is the only source of spatial movement in the ecological gradient models (except for a small Gaussian value that displaces offspring from their mother's location). Of course, in non-spatial models movement can be ignored, since every individual has unrestricted access to the entire environment.

(a) Individuals

Individuals are characterized by a haploid genotype and a phenotype. A phenotype consists of two independent quantitative traits with a corresponding set of n bi-allelic (0 and 1) additive loci. T_{eco} defines the ecological trait with $n = 100$ loci. Since this is a study based on the magic-trait model, T_{eco} is also the target of female mate choice. In a small subset of experiments that explore two-trait dynamics, an independent mating trait (T_{mate}) is the target of female mate choice instead. $T_{mate\text{-}range}$ defines the trait that encodes reproductive isolation (see subsection (c) below) with $n = 5$ loci. Trait values are generated by simply adding up all 1's in the respective gene. Trait values t_i thus fall in the range $0 \leq t_i \leq n_i$. This genotype-encoding scheme follows other models with explicit genetics such as Dieckmann and Doebeli (1999), Doebeli and Dieckmann (2003) and Kawata (2001).

Regarding the implementation of genotypes it is important to highlight the way '1' alleles are distributed in genotypes of the first generation. Trait values are initialized to a defined value (see initial conditions) and an according number of '1' alleles is placed at consecutive loci starting at the first locus. This encoding scheme ensures a monomorphic initial population. If '1' alleles were distributed randomly among all loci, one would have a system with a maximum number of polymorphic loci and thus maximum genetic variance (see mating trait in D&D models). Under such circumstances, a chance mating of two individuals with complementary genotypes could produce offspring of maximum and minimum phenotypic value in the earliest stages of a simulation. Speciation would thus experience an unrealistic, model-implementation-dependent boost.

Individuals feed, reproduce and move, and their phenotypes are constructed to conform to these requirements. Each individual is characterized by an evolving ecological trait T_{eco} and a fixed ecological range a_{eco} (centred on its T_{eco}) that defines the range of food objects it can feed on and determines the competitive overlap between individuals. Small values of the ecological range indicate specialist individuals and large values generalist individuals. Ackermann and Doebeli (2004) operate with a similar niche position (T_{eco}) and niche width (a_{eco}) encoding, with the exception that in my model a_{eco} does not evolve.

Whether an agent is able to eat a certain food object is determined by the food object's location (applies only to ecological gradient environment) and phenotypic value. In the case of the spatially explicit gradient setting, a list of geographically close food objects is generated first for each randomly chosen feeding individual. The maximum spatial distance of a food object an individual can investigate is *m*; that is, an individual can scour for food in a spatial perimeter defined by its own location $L_{indiv} \pm m$. Such a threshold rule is chosen for computational simplicity. A Gaussian distance rule produces qualitatively similar results.

In a second step, this individual then selects a phenotypically suitable food object from this list of spatially close food objects. Step one is omitted in simulations with the non-spatial Gaussian environment. Step two proceeds as follows. An availability-value is drawn from a Gaussian distribution with ($\mu = a_{eco}$; $\sigma = 1.0$). If the actual distance between an agent's T_{eco} and the food object is smaller than the availability-value, the agent will eat the food object. Such an eating behaviour has the character of a threshold strategy where agents can eat any food objects within a certain phenotypic range and nothing beyond that range. This encoding may appear idiosyncratic but it ensures greater control in identifying the influence of a_{eco} on speciation dynamics.

Simulations have also been performed using the standard 'Gaussian' eating behaviour where the likelihood of food uptake of an agent declines gradually with phenotypic distance. In this case, an availability-value is drawn from a Gaussian distribution with ($\mu = 0$; $\sigma = a_{eco}$). If the actual distance between an agent's T_{eco} and the food object is smaller than the availability-value, the agent will eat the food object. In terms of running simulations, it is worth noting that parameter values for a_{eco} need to be smaller for the Gaussian strategy than for the threshold strategy. The above two foraging strategies should be considered alternatives until empirical research has identified one of the two as the strategy employed by real animals.

(b) Environment

Two environmental settings have been implemented: (1) a non-spatial environment with a Gaussian distribution (according to phenotype) of food objects and (2) a spatially explicit ecological gradient environment (see Fig. 1).

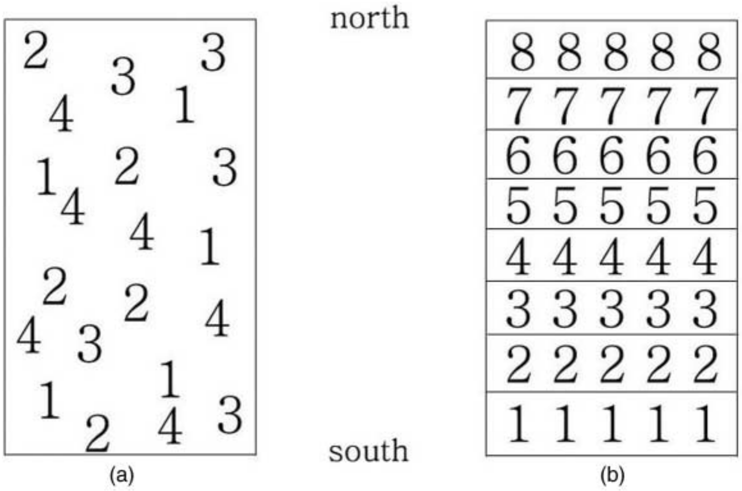


Fig. 1. Spatial distribution of food objects: (a) randomly placed in the environment in the non-spatial setting and (b) assortatively placed in patches along the south–north oriented x-axis in the ecological gradient setting. Numbers indicate food objects of different phenotypic value.

Food objects have a one-dimensional 'phenotypic' value P_{food} (such as size or colour) and a location x (only expressed in spatial models). In the non-spatial model, phenotypic values of food objects are drawn from a Gaussian distribution ($\mu = 50$; $\sigma = 25$) and are randomly placed in the environment (Fig. 1a). A different food distribution is required for the spatially explicit gradient ecological scenario. Here, a fixed amount of *n* food objects is placed in a one-dimensional patch with width d_{patch}. Patch-specific phenotypic values increase along the x-dimension (south–north direction) producing an ecological gradient (Fig. 1b). A typical gradient used in most simulations contains 20 patches each with 30 food objects. Once a distribution (unimodal or gradient) has been established, it will be reset to its original state every generation. This, in effect, ensures that all generations of a simulation face the same ecological conditions.

In all spatial simulations investigated here, the environment individuals operate in expands along only one dimension. The 'size' of an environment is fixed at 120 units resulting in 120 possible different geographical locations.

(c) Mate search tactics

Speciation dynamics with two evolvable mate search tactics have been investigated for this study. The aim is to compare the assortative mating performance of the best-of-*n* and threshold mating tactics. Characteristic for both these mating tactics in all simulations is that a lek of *n* randomly chosen males is produced and then presented to a female. Every female gets her own, individual lek.

Females pick a mate according to the closest phenotypic distance in the best-of-*n* tactic. The male that is closest to the female will be picked as that female's mate. To model the evolution of reproductive isolation, an evolving 'fuzziness' value is added to the distance measurement conducted by each female. This fuzziness value is defined by a female's $T_{mate\text{-}range}$ and initially set to a high value to achieve random mating. For speciation to occur, $T_{mate\text{-}range}$ has to evolve to a very small value resulting in an accurate distance assessment on the side of females.

Phenotypic distance is also the crucial attractiveness factor in the threshold mating tactics. In this scenario, however, a female will pick any male that exists within the phenotypic neighbourhood (defined by $T_{mate\text{-}range}$) of that female. This threshold value is allowed to evolve and is initially set to a high value (large phenotypic neighbourhood) to ensure random mating. The threshold value again has to evolve to a small value to provide favourable circumstances for speciation. If no male inhabits a female's phenotypic neighbourhood, she picks a male randomly from her lek.

$T_{mate\text{-}range}$ is calculated as $T_{mate\text{-}range} = [\sum_{i=1}^{5} l_i]^2$ in both mate search rules. In case of the best-of-*n* rule, this means that the distance judgement of a female is drawn from a Gaussian distribution with $\mu = T_{eco}$ and $\sigma = T_{mate\text{-}range}$. The smaller $T_{mate\text{-}range}$ becomes, the more accurate a female's judgement is and the more likely she mates assortatively. For the threshold rule, a female's acceptance threshold is calculated as $T_{mate\text{-}range}$ plus a small Gaussian value.

RESULTS

One of the most visible results of this study is the dynamic nature of population divergence (see Table 2). In many parameter settings, sub-clusters form and get swallowed up again.

Other scenarios show a gradual increase of cluster number over time as the population explores a wider range of the environment. Waiting time to speciation (i.e. in those circumstances where it does occur) or to the forming of a (resource) polymorphism is also highly variable in many parameter combinations.

This section consists of three parts. The first part verifies that indeed competition and assortative mating are implicated in speciation. The next part covers the issues discussed in the 'Goals of this study' section (summarized in Table 2). Best-of-*n* is shown to be much more effective in driving population divergence. It is further shown that a monomorphic population can undergo sympatric speciation to completion and that clustering may also occur in the centre of the food distribution depending on the actual value of competitive overlap. The final part reports additional results – (1) individuals do not speciate in geographical space and (2) maximum lek size (females select mates from the entire male population) has a detrimental effect on speciation – and addresses the problem of whether reproductive isolation does actually evolve. Reproductive isolation does evolve with the best-of-*n* search rule but not with the threshold rule.

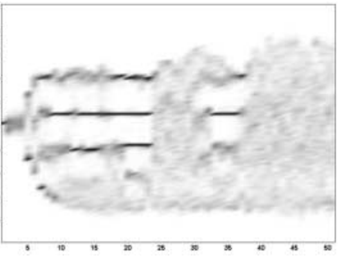
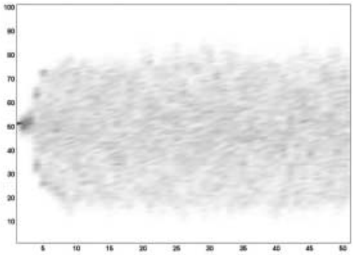
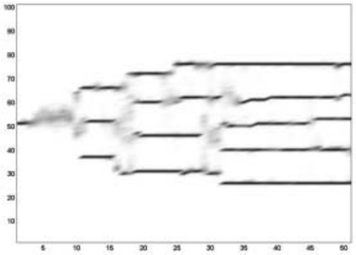
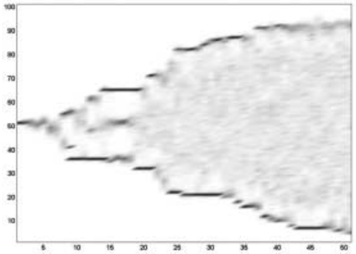
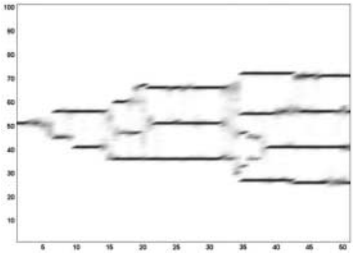
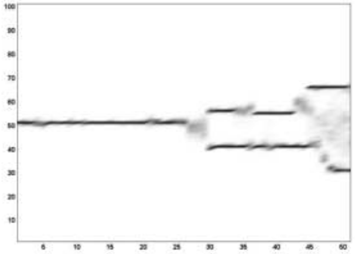
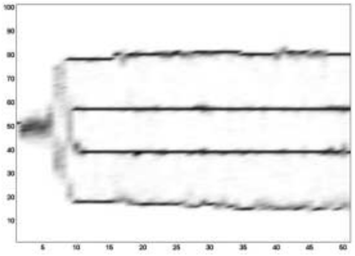
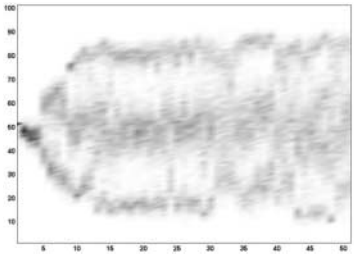
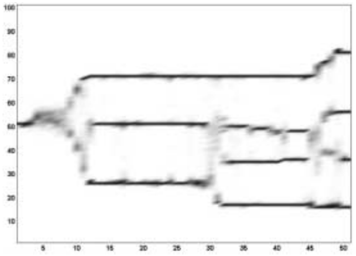
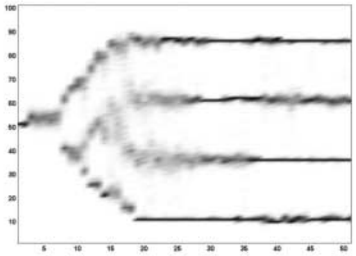
The basic simulation set-up for most results reported in this section refers to a generational model with each simulation run lasting 5000 generations. A population census was taken every one-hundredth generation and the frequency distribution of phenotypic values calculated and drawn. Carrying capacity was set to 600 individuals (i.e. there are 600 food objects in the environment) in both the non-spatial and the spatial ecological setting. A monomorphic population was produced with initial ecological phenotypic values set to the mean of the food distribution in the unimodal non-spatial model and to the central value in the gradient ecological setting. Individuals were placed in the middle sector of the ecological gradient. Competitive overlap a_{eco} between individuals is the same for all simulations reported below (except in the non-competition simulation). Investigated values range from extreme specialists ($a_{eco} = 5$) to generalists ($a_{eco} = 40$) with intermediate values of $a_{eco} = \{10, 15, 20, 30\}$.

All figures presented here present a typical simulation run and not the average dynamics over several simulation runs. This is done deliberately because there is no such biological entity as an 'average species'. Averaging will mask potentially interesting stochastic effects that could be biologically important (see alternative cluster configurations in Table 2). Agent-based models such as the one used here are particularly successful in producing chance events that might be worth studying in themselves. However, one has to ensure that those stochastic effects are bounded in that 'typical' dynamics can be identified. If no categories of scenarios emerge, no useful analysis of results would be possible. The results of this study are characterized by clear boundaries, although individual runs within these boundaries show marked differences. Certain search tactics, for example, consistently produce the same sequential bursts of cloud-like clusters of individuals while at the same time their overall dynamics can still be classified into one category.

All figures shown in this section depict time in the form of generations (5000) on the x-axis and phenotypic values for T_{eco} on the y-axis ([0, 100]).

It is important to note that all reported results in this chapter were obtained with the threshold foraging strategy where agents are able to eat any food object within a certain phenotypic range. Additional simulations with the Gaussian foraging strategy have essentially produced the same results. Discrepancies between the two foraging strategies are only visible for larger a_{eco} values in the non-spatial Gaussian environmental setting. Whereas speciation occurs with the threshold strategy, no population divergence evolves with the

Table 2. Results of the two mate search tactics in both environmental settings

a_{eco}	Gaussian food distribution with best-of-*n*	Gaussian food distribution with threshold	Gradient food distribution with best-of-*n*	Gradient food distribution with threshold
5				
				
10				

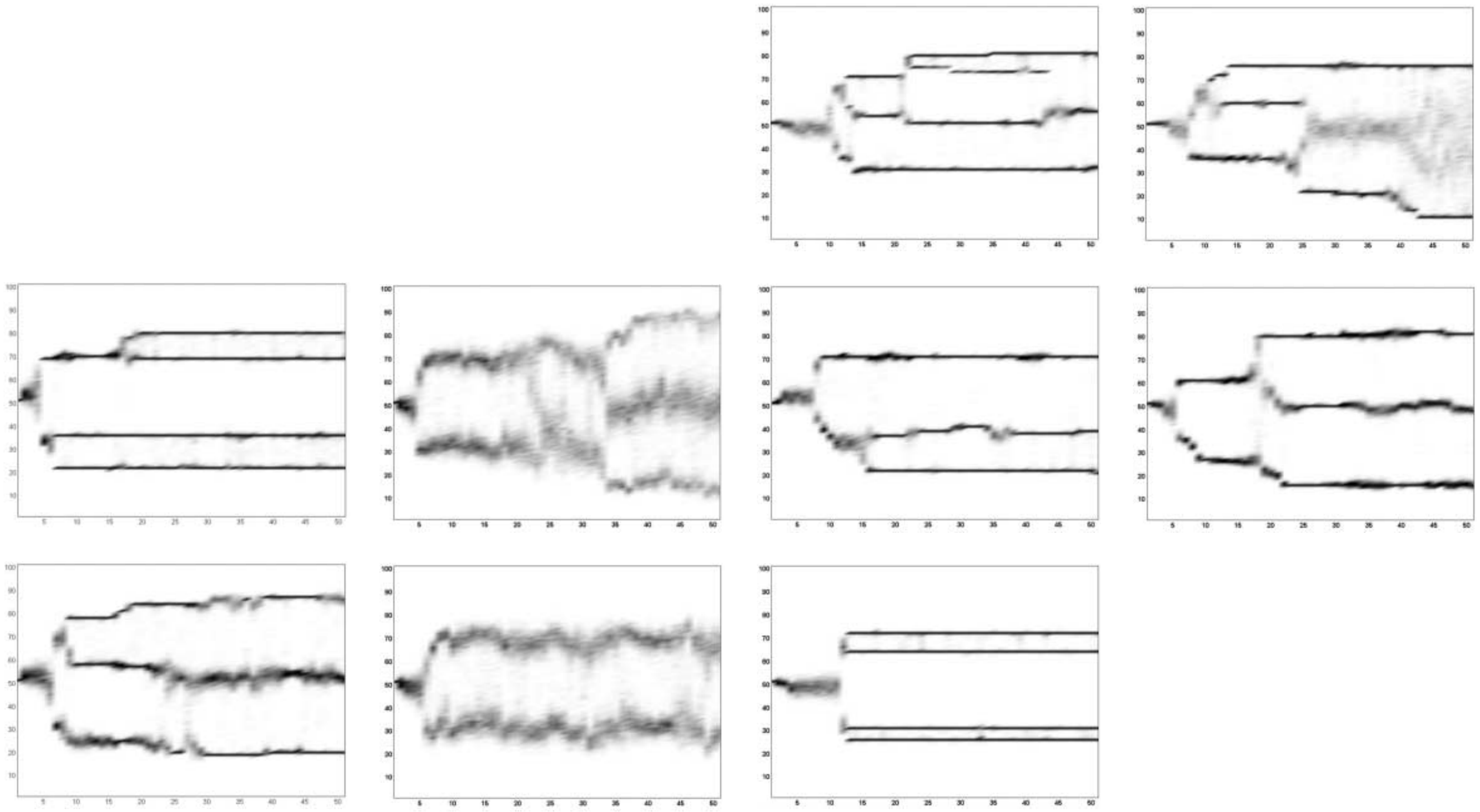

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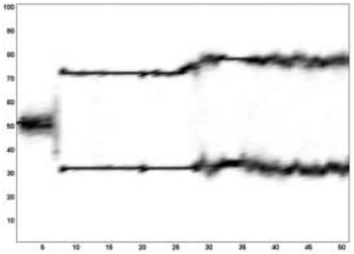
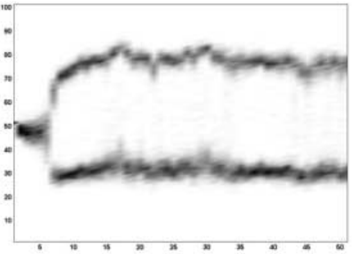
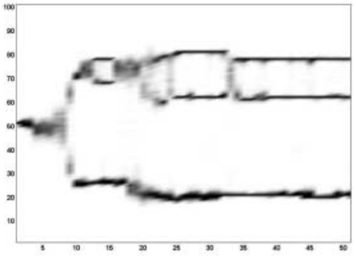
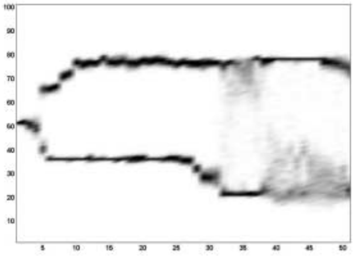
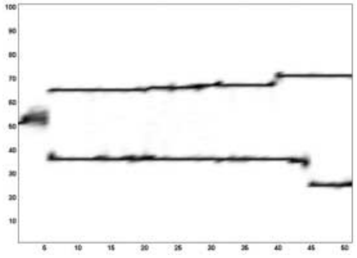
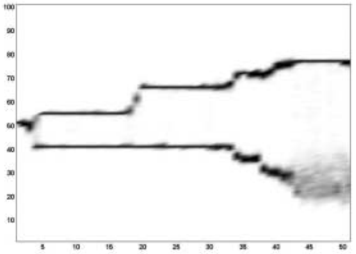
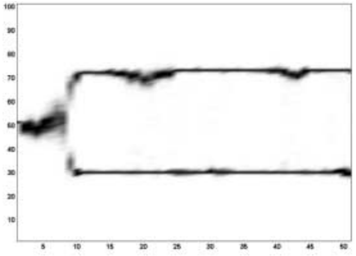
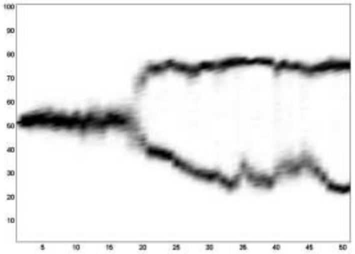
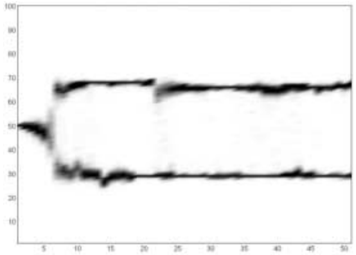
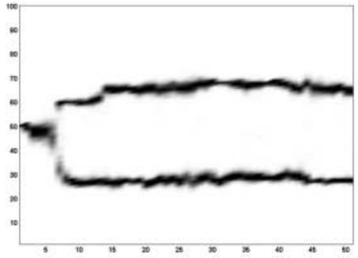
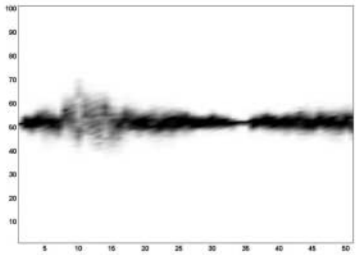
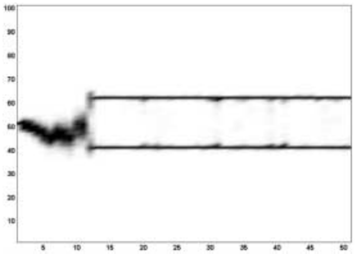
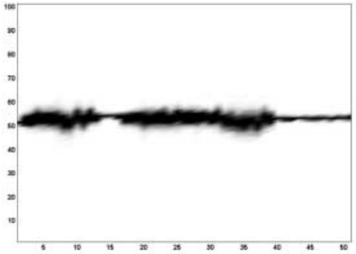
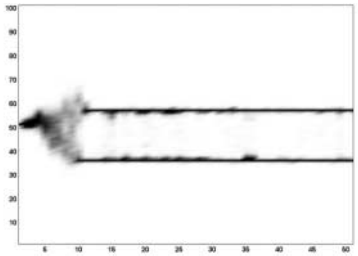
Table 2.—*continued*

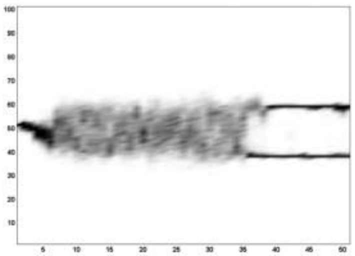
a_{eco}	Gaussian food distribution with best-of-*n*	Gaussian food distribution with threshold	Gradient food distribution with best-of-*n*	Gradient food distribution with threshold
20				
				
30				

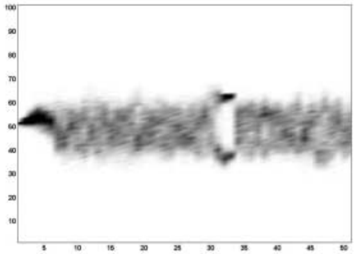


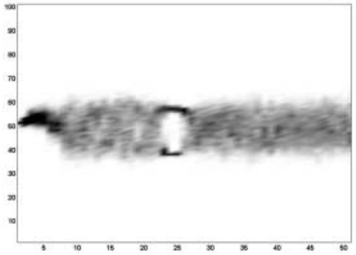












Note: Two pictures in a cell indicate two alternative cluster topologies for a given a_{eco}.

standard Gaussian strategy. This discrepancy can be explained with the implicit 'resource partitioning effect' of the threshold strategy. Although agents scour the entire environment for food, they only have access to those food objects that fall within their foraging range. In case of the Gaussian foraging strategy, agents will eat phenotypically distant food objects with a small probability. With larger values, agents 'eat out' (of their range) too often with the result that any form of population divergence is completely inhibited.

The fact that both foraging strategies essentially produce the same cluster formations highlights the robustness of the present results.

1. Effect of competition-absence and random mating

Competitive speciation is based on the notion that competition for a limited resource functions as disruptive selection. Sympatric speciation theories stress the importance of assortative mating during the process of population divergence (Kondrashov, 1986; Turelli *et al.*, 2001; Coyne and Orr, 2004). To test these two factors, control simulations were run with (a) competition turned off and (b) random mating instead of evolvable assortative mating. Both these control simulations confirm the above two contentions. Random mating as well as the absence of competition lead to the evolution of a limited polymorphism (see Fig. 2a and 2b). As these images reveal, competition does indeed drive the generation of a genetic variance in the population that in the absence of assortative cannot lead to speciation.

2. Effect of mate search tactic and general speciation dynamics

Population dynamics driven by competition for a limited resource exhibits several patterns that are the product of interactions between three variables: (1) ecological setting, (2) ecological range of individuals (a_{eco}) and (3) mate search tactic employed by females. As a first approximation, one can conclude that the ecological gradient environment is more facilitative for clustering than the environment with a continuous food distribution. Furthermore, best-of-*n* search is a more conducive mate search tactic than threshold search and is less influenced by the effect of different environmental conditions. Finally, the average cluster distance and number is a function of a_{eco} with larger values of ecological range producing fewer population clusters and smaller values producing more population clusters. For a detailed depiction of the results, see Table 2.

The general trend of best-of-*n* outperforming threshold mating can be observed for all ecological ranges in an environment with a continuous resource distribution and for highly specialist creatures ($a_{eco} = 5$) in an ecological gradient environment. Clustering occurs with best-of-*n* mating in the continuous environment for all values of a_{eco} with the exception of highly specialized creatures ($a_{eco} = 5$), in which case clustering is temporary and partial (clusters show different evolutionary patterns of birth and extinction). Smaller values of a_{eco} result in stronger frequency dependence and should promote speciation. The observed temporal and partial clustering (instead of speciation) can be explained with the randomizing effect of the implemented lek-mating system in my model. With very small a_{eco} values, males with very similar phenotypes are likely to enter a lek. A female will then mate randomly within a small section of phenotype space. This 'constrained random mating' in the Gaussian environmental setting is powerful enough to prevent clustering. Limits on mobility in the ecological gradient setting produces pre-filtered male leks according to phenotype and females will thus always mate assortatively. Constrained random mating

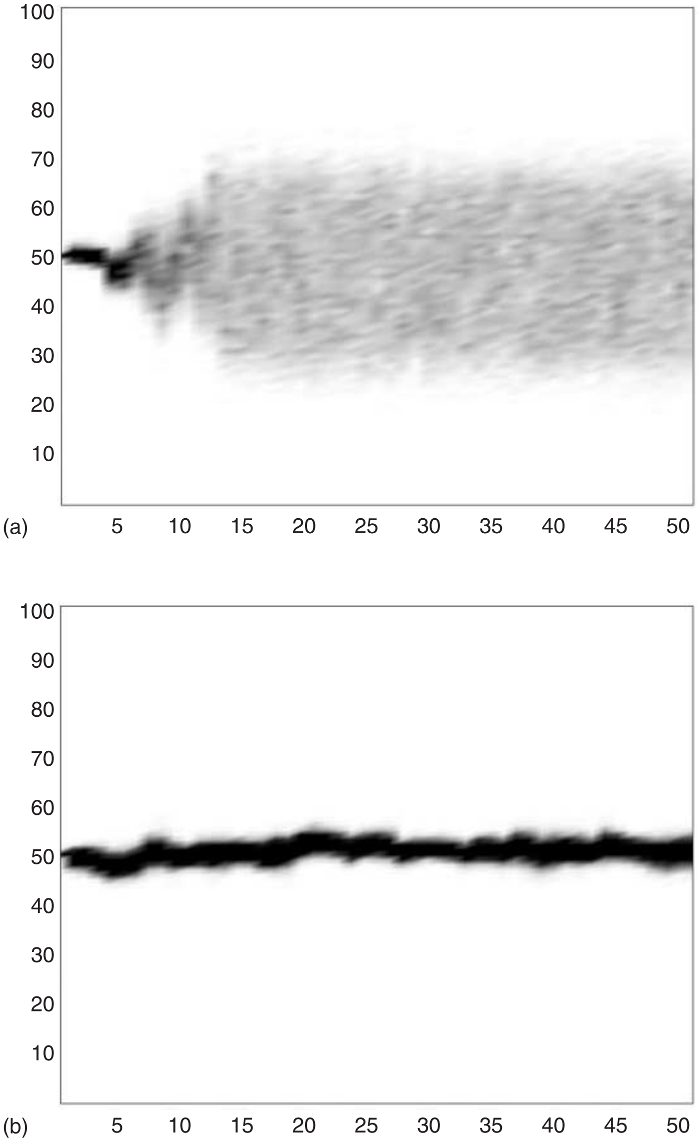


Fig. 2. Population dynamics with (a) random mating and (b) no competition between individuals.

does take place in the ecological gradient setting and stable clustering now also evolves for highly specialized creatures.

Threshold mating shows a much higher degree of dependency on ecological condition. Distinct clusters will evolve only for intermediate ecological range values ($a_{eco} = \{15, 20\}$) and with about 50% chance with $a_{eco} = 30$ in the Gaussian environmental setting. The observed dynamics for $a_{eco} = \{15, 20\}$ could be interpreted as incipient speciation but no definite decision can be made without quantifying the allowed gene flow (for incipient speciation) between clusters. Since this is not known in my model, a conservative conclusion can be drawn that only a stable resource polymorphism has evolved. With extreme values we find either an unstructured polymorphism ($a_{eco} = 5$) or a phenotypically static population ($a_{eco} = 40$). Clustering does occur with $a_{eco} = 10$ but cluster boundaries are highly permeable and the resulting profile resembles a very weak resource polymorphism.

Threshold mating receives a considerable boost in causing population divergence in an environment with an ecological gradient. Clustering now occurs for all a_{eco} values but evolving profiles still depend on the degree of ecological specialization of creatures. Populations of highly specialized individuals ($a_{eco} = 5$) do diverge into distinct clusters but these lineages collapse after a couple of hundred generations into an unstructured polymorphism. A similar evolutionary fate is possible with $a_{eco} = 10$ but in about 50% of the cases lineages will co-exist as distinct evolutionary trajectories. Intermediate ecological ranges ($a_{eco} = \{15, 20, 30\}$) consistently produce stable clustering constellations.

Three interesting patterns can be identified that cannot be predicted from theoretical considerations of the identified key system parameters (ecological condition, mate search tactic and ecological range). First, evolved clusters for generalist populations ($a_{eco} = \{30, 40\}$) are phenotypically closer together than would be necessary for the absence of competition between populations. Clusters are permanently stable with $a_{eco} = 30$ but only temporarily stable for $a_{eco} = 40$. This lineage constellation could be an evolutionary compromise between the scarcity of food objects in distribution regions where competitive exclusion would place clusters at the minimum distance that is required to co-exist as different sub-populations.

A second non-intuitive finding refers to the similar cluster profiles of both mate search tactics for generalist populations ($a_{eco} = \{30, 40\}$). This is particularly evident in the ecological gradient condition but already visible for $a_{eco} = 30$ in the Gaussian food distribution setting. Finally, intermediate ecological range values ($a_{eco} = \{15, 20\}$) in connection with best-of-*n* mating result in bi-cluster constellations with additional satellite clusters that may accompany both main clusters ($a_{eco} = 15$) or only one of the two main clusters ($a_{eco} = 20$). These satellite clusters are of particular interest because their distance to their respective main cluster puts them in constant competition with these main clusters. A similar explanation as the one for the existence of clusters in generalist populations ($a_{eco} = \{30, 40\}$) may apply to the existence of satellite clusters.

In this context it should be mentioned that the evolved cluster topology (e.g. number of clusters) does not change with the width of the food distribution. Additional experiments that were performed with a food distribution width of $\sigma = 15$ (instead of the default $\sigma = 25$) only resulted in an expected more constrained exploration of the extreme regions (very small and very large values for T_{eco}) of phenotype space but not in a change of cluster constellations. This result highlights the importance of a_{eco} as the basic factor in partitioning the resource space. Cluster topology (stable locations of species in phenotype space) is only dependent on the individual foraging strategy in a population (a_{eco}) and not on the width of the resource distribution.

Competition between individuals in the present model is determined by the foraging strategy (a_{eco}) employed by individuals. As mentioned in the Introduction, such a biologically realistic implementation of competition implicitly partitions the available resource space and thus explains the above results. D&D models (1999, 2003), in contrast, feature ‘only’ a direct implementation of competition without any notion of an ecological range (niche width). This difference in modelling competition is responsible for the fact that my study did not find any dependence of the likelihood of speciation on the strength of competition between individuals and the carrying capacity of the environment (speciation only occurs if $\sigma_c < \sigma_K$) as reported by Dieckmann and Doebeli (1999).

3. Spatial distribution

D&D report ‘spatial’ speciation in parallel to phenotypic speciation in their spatially explicit gradient model (Doebeli and Dieckmann, 2004). No such spatial clustering evolves in simulations with an ecological gradient performed for this study. Unlike the phenotypic and spatial distribution isomorphism presented by D&D, this study finds a spatial polymorphism with individuals occupying parts of the ecological gradient or the entire ecological gradient. A very small a_{eco} produces a smaller spatial expansion than larger a_{eco} values. Individuals do segregate into spatial clouds corresponding to their phenotypic values (individuals with large phenotypic values are located in the north and vice versa; see Fig. 3) but these clouds overlap resulting in a spatial polymorphism and not speciation.

This spatial polymorphism is a rather counterintuitive result (M. Doebeli, personal communication) and requires some explaining. Individuals have a certain degree of mobility m that defines the geographical area they can scour for food and mates. They are also characterized by an ecological range a_{eco} that defines the range of nuts they can eat. These two parameters are responsible for the continuous spatial distribution because individuals do not have to be immediate geographical neighbours to feed on the same nuts (to be precise, on nuts of the same size). In other words, individuals of very similar phenotype can be geographically apart. Phenotypic speciation now is the result of best-of-n induced assortative mating. As long as the distance between individuals of similar phenotype does not exceed m, they are within each other’s geographical mating range (leks for females are generated only from males that are geographically close). That geographically distant individuals nonetheless cluster phenotypically is thus the result of best-of-n mating.

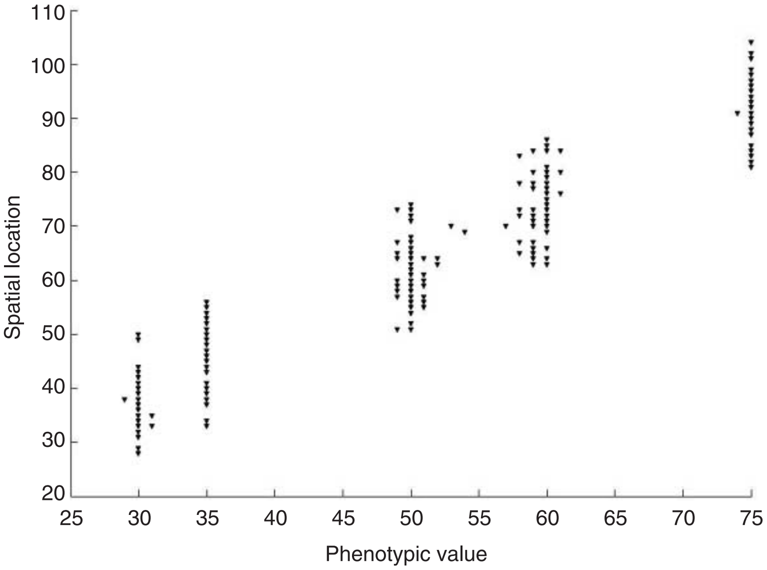


Fig. 3. Individuals segregate into spatially overlapping but phenotypically distinct clusters in the ecological gradient setting; shown is a scatter-plot of generation 5000 with $a_{eco} = 5$.

4. Has reproductive isolation evolved?

Assortative mating in D&D models has evolved when most females carry only plus alleles at their mating loci. Mating probability then is indirectly proportional to phenotypic distance. In the models presented here, it is fuzziness of distance assessment that evolves and once most females are very accurate, assortative mating is assumed, for the purpose of this paper, to have evolved. As Fig. 4 shows, this is indeed the case with the best-of-*n* mate search tactic.

However, there is an inherent problem with any best-of-*n* implementation. In D&D models, females are presented with the entire male population with the effect that a female will always pick a male from her cluster (given an evolved cluster structure in a diverged population). Females in real natural situations have hardly ever the opportunity to sample all males of their population. Limited time and other constraining factors (e.g. predators) will reduce the sample size of selectable males. These constraints are captured with the lek mating system implemented in the agent-based models presented here. A lek of *n* randomly chosen males may by chance only contain males of the opposite cluster C2 (assuming a system with two clusters C1 and C2). A C1 female confronted with such a lek of C2 males will still pick the closest male and will thus mate 'assortatively'. Complete premating isolation, however, does not exist in such circumstances.

The question of whether complete premating reproductive isolation may evolve with a best-of-*n* mate search tactic has to be negated unless some other reproductive isolation barrier (premating, postmating/prezygotic, postzygotic) evolves concomitantly to prevent accepting a lek of 'foreign' males or of producing fit offspring. However, as the results clearly show, speciation is highly likely with best-of-*n* mating with appropriate values of competitive overlap. This finding indicates that complete reproductive isolation is not necessary for the evolution of new species as long as females mate accurately within their cluster most of the time.

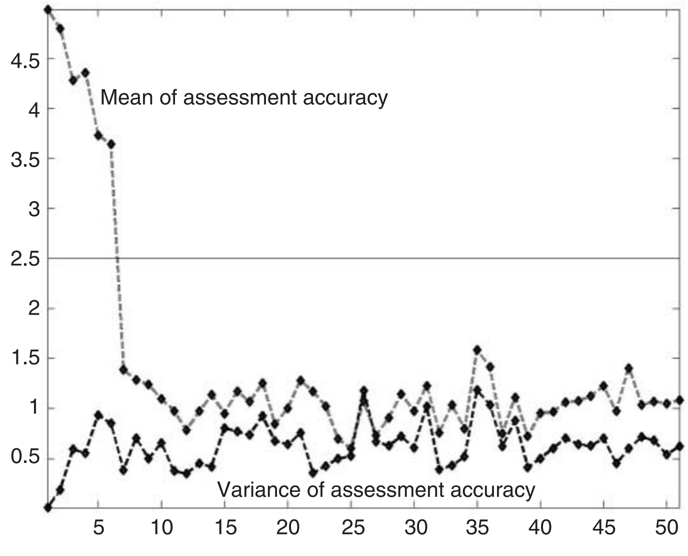


Fig. 4. Mean and variance of assessment accuracy of females using best-of-*n* rule. The x-axis shows time in generations × 100; the y-axis shows the phenotypic value for mean and variance.

Threshold mating as implemented in this study poses a much harder problem regarding the evolution of reproductive isolation. Theoretically, reproductive isolation should evolve once the threshold has evolved to a value smaller than the distance between any two clusters, which in turn is determined by a_{eco}. The results, however, paint a very confusing picture. The mean threshold value does indeed drop to a value lower ($4 < T_{mate\text{-}range} < 12$) than the initial value ($T_{mate\text{-}range} = 25$) but it does so in polymorphism situations as well as in clustering situations. Such a value should be low enough to produce accurate assortative mating necessary for speciation. The question now is, why does speciation not occur in the Gaussian ecological setting despite a low enough mean threshold value? Compared with best-of-*n* mating, the results show a much higher variance in the population with threshold mating. A structured environment as it is present in the ecological gradient scenario provides additional selection pressure to frequency-dependent competition. These two forces together appear to be strong enough to cause speciation despite the high variance. Since a structured environment is absent in the Gaussian food distribution scenario, one form of selection is missing and speciation accordingly does not evolve.

5. Effect of lek size

To test whether small lek size is a contributing factor to stochasticity (local clustering and extinction events) during speciation, simulations were conducted with the highest lek size value possible. In this setting, each female is presented with all males in the population in the non-spatial ecological scenario and with all males in her spatial vicinity in the gradient scenario. Based on the foreign males cluster argument presented in (4) above, one would expect that with a much larger number of males in a lek, speciation (in cases where it actually occurs) would proceed in a more stable, equilibrialized manner. Results produced for this section, however, show the exact opposite effect in the best-of-*n* mate search tactic and a catastrophic effect in the threshold case. A population appears paralysed in phenotype space over time with occasional short phenotypic distance movements in a situation where females pick mates according to the threshold rule (Fig. 5a). With best-of-*n* as the mate search tactic, divergence becomes a much more fickle and temporary affair with many local small-scale clustering and extinction events (Fig. 5b). This effect is observed in both ecological settings.

6. Effect of genetic architecture of traits

Population divergence with a magic trait system is considered the strongest contender for speciation but also the least plausible one (Coyne and Orr, 2004). Biologically more realistic is a two-trait system with independent ecological and mating traits. D&D report that in both their non-spatial (Dieckmann and Doebeli, 1999) and spatially explicit (Doebeli and Dieckmann, 2003) models, speciation does occur. To test whether a similar outcome can be reproduced with the agent-based model, additional simulations were run with a two-trait system. Results indicate that sympatric speciation does occur in two-trait systems in my agent-based model, albeit under a much smaller range of parameter settings than in the magic-trait condition.

Population divergence was not observed in the Gaussian food distribution scenario. Individuals explore a wide range of phenotype space but do not form clusters. This applies to both mate search tactics. Additional selection pressure of a structured environment in

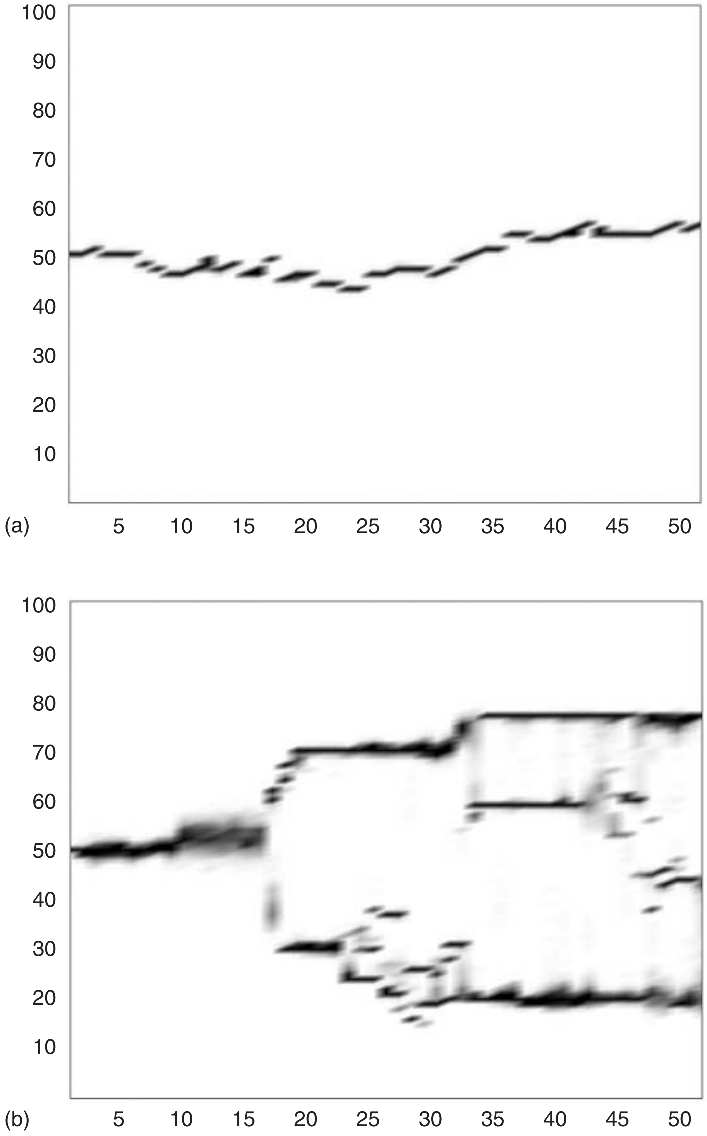


Fig. 5. Mate choice without lek: (a) threshold tactic, (b) best-of-*n* tactic.

the gradient scenario allowed cluster formation in a very small range of a_{eco} values with best-of-*n* mating. The threshold rule again only resulted in an unstructured polymorphism.

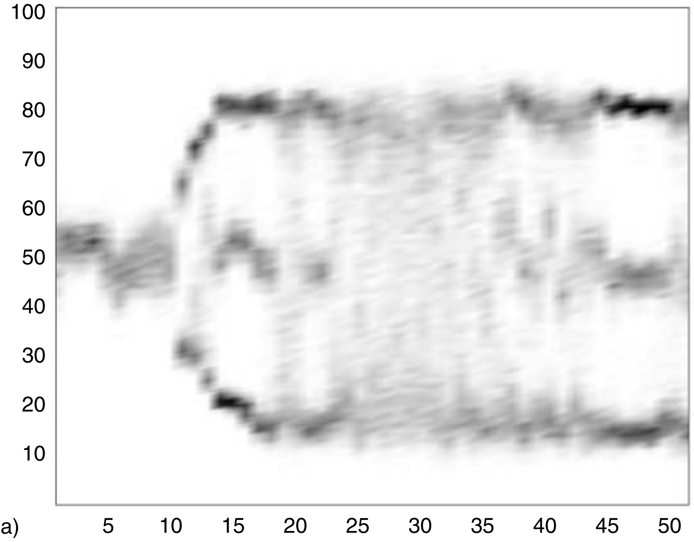
Figure 6 depicts typical speciation dynamics with a two-trait system and a medium value (= 15) for a_{eco}. Whereas the evolved three-cluster constellation is only temporally stable in Fig. 6a, we see a stable two-species system in Fig. 6b. The major difference between simulations that produced the dynamics in Fig. 6 is the underlying mating system: (a) the default lekking system and (b) an additional lek-free system. Females had only restricted access to potential male mates in the lekking mating system (lek size = 20) that produced the constellation in Fig. 6a. A mating system with unrestricted access (i.e. any given female could sample the entire male population) to potential mates, on the other hand, produced a bi-cluster constellation in about 40% of simulation runs. It is interesting to note that the corresponding mating trait dynamics (Fig. 6c) are very different in character and show strong effects of drift and gene-flow between clusters. A possible interpretation of this is that only a strong temporal linkage-disequilibrium between the ecological and mating traits is required to split a population and that the mating trait then develops its own, independent evolutionary trajectory.

Other studies have assumed a high genetic variance in key traits and it has been argued that such a high variance might be conducive for speciation (Waxman and Gavrilets, 2005). The results obtained here in further two-trait simulations indicate that this effect is very limited in my model. High variance simulations did not change the results for the Gaussian food distribution and the threshold mating in conjunction with an ecological gradient. Cluster formation was more distinct in a best-of-*n* mating system operating in an ecological gradient setting. These results did not change when simulations were run for 10,000 generations.

Finally, all simulations reported so far were based on an evolvable assortative mating system. Simulations were also run with *a priori* assumed assortative mating. Such a constellation with assortative mating built into the simulation readily leads to speciation in two-trait systems with best-of-*n* mating in my model. Results in this section provide further evidence that speciation in two-trait systems is possible. Parameter values in my model are more restricted than those reported in D&D (1999) but the same overall phenomenon was nonetheless observed. The key factor determining population dynamics in my model is the underlying mating system. No stable speciation occurs with the default lekking system. Speciation does occur with a certain probability in an unrestricted mating system (no leks) and it always occurs in simulations with assumed assortative mating.

DISCUSSION

Sympatric speciation is a vain mistress to please with very particular requirements. Agent-based modelling proves to be a versatile methodology in the study of complex natural systems such as this vain creature. Simulation runs revealed an interesting degree of stochasticity, although only a few variables such as mate search tactic, competitive overlap and lek size were able to interact. Results fall into categories but intra-category variance indicates the range of population dynamics that are evolutionarily possible with a particular set of variables. These diverse members of result categories manifest an improvement over results obtained with analytical and simple individual-based models. Many natural systems are likely not to be equilibrium systems and are thus characterized by the existence of stochastic events. Agent-based modelling with its bottom-up approach is able to capture the essence of those stochastic events very well (Railsback, 2001). The downside, of course, is that results are harder to interpret (Wheeler *et al.*, 2002). Another characteristic of agent-based models (including mine) is an emphasis on specificity and biological realism. D&D models (1999, 2003), on the other hand, emphasize simplicity and generality. Their individual-oriented models and my agent-based model should therefore be considered alternative approaches.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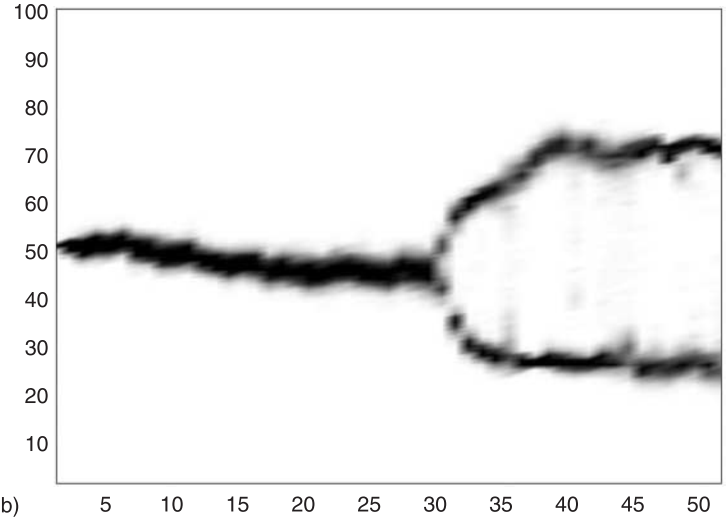
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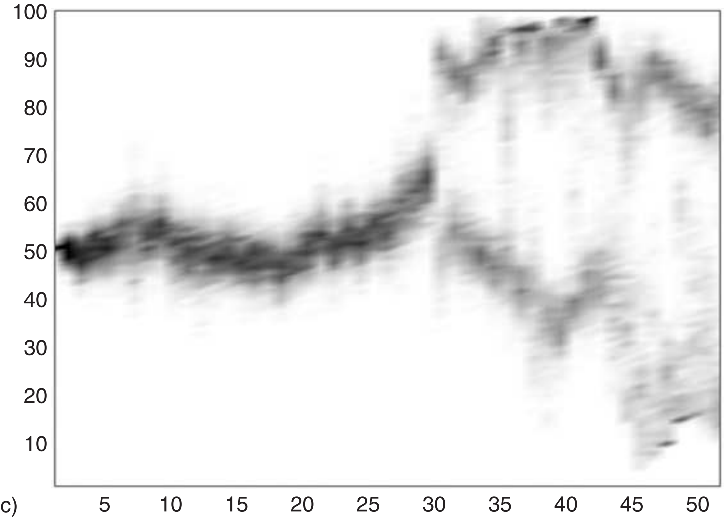
(b)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(c)

This study confirms certain results of earlier studies, presents results differing from those of previous studies and extends the scope of competitive speciation models by introducing a more realistic mating system (different mate search tactics and leks) and an explicit implementation of food resources. Confirmed results include the power of competition as a disruptive force and the positive effect of a structured environment such as an ecological gradient on speciation dynamics. The agent-based model implemented for this study allowed me to re-analyse in more detail results of the D&D models. The following only applies to best-of-n mating. Several key findings stand out.

First, a monomorphic population can proceed through both phases of sympatric speciation to completion and reproductive isolation. These results are robust and independent of the underlying implementation of the actual foraging strategy (threshold or Gaussian), except for large a_{eco} values in the Gaussian case. Robustness of results is a good indicator that the present results are not artificial products of my specific model set-up but that they describe actual phenomena. A note is in place concerning the distribution in the initial population of the ecological range a_{eco}. Every individual in all of my simulations shares the same ecological range value making a population monomorphic on this character. This may seem to be a biased oversimplification but was done with a reason. In simulation runs with an evolvable a_{eco} and with initial values drawn from a Gaussian distribution, this value very quickly (within the first couple of hundred generations) converged on the largest value that was initially present. No speciation events were accordingly observed in this 'convergence' scenario. My model does not feature a cost for being a generalist and it is thus no surprise that the most generalist strategy becomes fixed in a population. This result is similar to the findings of Ackermann and Doebeli (2004), who also did not observe adaptive speciation with an evolvable a_{eco} (they refer to it as 'niche width' of an individual) and no or little cost attached to being a generalist.

The major difference between their study and mine is that Ackermann and Doebeli (2004) modelled an asexual population whereas I model a sexual population where assortative mating has to evolve. In the observed convergence scenario, assortative mating did not evolve and one of the basic requirements for sympatric speciation was thus not in place. Based on my results, it appears that there exists an antagonistic relationship between the evolution of competitive overlap a_{eco} (or niche width) and the evolution of assortative mating. More research is needed to disentangle this relationship. My model, for example, does not incorporate any cost for being a generalist. A combination of the Ackermann and Doebeli (2004) generalist cost assumption and a sexual individual-based model of competitive speciation would be a good starting point.

Second, clustering may also occur in the centre of the food distribution depending on the actual value of competitive overlap. Third, the average distance between clusters depends on the actual value of competitive overlap except for the largest implemented values where clustering occurs well within the competitive range of individuals (i.e. with overlapping niche widths). D&D did not find multiple speciation events in their non-spatial model (1999) and briefly hint at them in their spatial model (2003, legend to figure 3). However, D&D (1999, 2003) only consider the general requirement for adaptive speciation where the width of

Fig. 6. Dynamics with independent ecological and mating traits in the ecological gradient condition and $a_{eco} = 15$: (a) mating with lek (shown is T_{eco}); (b) mating without lek (shown is T_{eco}); (c) same as (b) but T_{mate} is shown.

the competition distribution is smaller than the width of the carrying capacity ($\sigma_c < \sigma_K$). They do not investigate in detail the effects of progressively smaller values for σ_c. My results show that multiple speciation events only occur for small to intermediate ecological range values (niche widths) and that bi-cluster constellations evolve with larger values. Ackermann and Doebeli (2004) also report multiple speciation events in the case of high costs for generalists resulting in a population of specialist individuals with small niche widths.

Fourth, a population does not speciate in geographical space resulting in constant competitive interactions of neighbouring individuals. This may explain the fine-grained cluster structure in the gradient scenario. Fifth, maximum lek size (females select a mate from all males) has a detrimental effect on speciation by causing many local temporary clustering and extinction events. Finally, speciation in two-trait systems where assortative mating has to evolve is possible in my model but depends on the ecological setting and on the degree of assortativeness that a given mating system allows. It never occurs in the non-spatial model and only under intermediate competitive overlap in the ecological gradient scenario. The evolved cluster constellation is unstable in the lekking mating system where females can only sample a subset of the entire male population. Such a lekking component adds a source of randomness to the mating behaviour of females. When females are allowed to sample the entire male population, evolved clusters are stable over time.

Assortative mating plays an integral part in sympatric speciation and detailed studies of different mate search tactics and different mating systems are almost completely absent from the theoretical speciation research map. The standard mating system employed in sympatric speciation models is an asymmetric one where males compete and females choose. One study that looked into the sympatric speciation dynamics of a mutual sexual selection mating system is that of Almeida and de Abreu (2003). This study investigated the two main classes of mate search tactic that have been discussed in the context of mate choice. Best-of-*n* mating where females pick the closest male to their preference (her ecological trait in a magic-trait scenario, an independent mating trait in a two-trait system) is a much more successful contender for speciation than threshold mating where females accept any male that exceeds a certain attractiveness value. Here we find an interesting interaction between individual decision making and environmental structure, since this advantage of best-of-*n* mating is drastically reduced in the ecological gradient scenario. However, any difference in population dynamics between mate search tactics and ecological scenarios vanishes when individuals employ a generalist feeding strategy. Clustering topology then looks very similar in both ecological settings.

Best-of-*n* mating presents an interesting theoretical modelling challenge. If one assumes a mating system where females only sample a subset of all available males, chance might force her to pick a male from a lek of only other-cluster males. Due to the nature of best-of-*n* mating, she will pick the closest male to her own phenotype disregarding the fact that all available males belong to a different species. Whether such a situation actually occurs in nature is unknown to the author. If not, nature has found a way of ‘pre-filtering’ inappropriate males according to a threshold rule. That said, the results show that potential gene flow caused by ‘other-cluster male’ leks might actually be healthy for speciation to occur. Simulations run with maximum size leks show a high degree of clustering noise caused by frequent splitting and extinction events.

Complete reproductive isolation cannot evolve with best-of-*n* mating due to the potential gene flow caused by ‘other-cluster male’ leks. Modern interpretations of the biological species concept accept low levels of gene flow (Coyne and Orr, 2004) and thus speciation has occurred in the present study in many of the simulations conducted with best-of-*n* mating. The results of this study are unfortunately ambiguous regarding the threshold tactic, since the threshold value evolves to a significantly lower than initial value but does so in clustering and in polymorphism situations. Simulation runs with the double-loci (for an explanation, see the Results section) genetic system confirm this trend. Clustering never occurs in either ecological setting. Based on these results, the present study has to conclude that speciation does not occur with threshold-based mating because reproductive isolation does not evolve.

Competitive sympatric speciation is not only a fashionable playground for theoretical modelling. Recent empirical studies show that competition does indeed function as a disruptive force in natural systems (Bolnick, 2004; Friesen *et al.*, 2004). A concerted effort of theorists and empiricists should now looks closer at the effects of individual decision making in the context of mate choice on speciation dynamics. Particular emphasis should be placed on two-trait systems with independent ecological and mating traits. A different topic in competitive speciation studies has received extremely little attention so far: multi-dimensional competition with several phenotypic traits. The only published study of a numerical model of *n*-dimensional competition is that of Vukics *et al.* (2003). *N*-dimensional competitive speciation has been studied as part of the PhD dissertation (Hilscher, 2005) this paper is based on. Results reveal that speciation in *n*-dimensional resource space is potentially very constrained. More research is clearly needed to extend our knowledge of *n*-dimensional competitive speciation.

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