International Institute for
Applied Systems Analysis
Schlossplatz 1
A-2361 Laxenburg, Austria

Tel: +43 2236 807 342
Fax: +43 2236 71313
E-mail: publications@iiasa.ac.at
Web: www.iiasa.ac.at

Interim Report **IR-05-022**

Adaptive Dynamics as a Mathematical Tool for Studying the Ecology of Speciation Processes

Michael Doebeli (doebeli@zoology.ubc.ca)
Ulf Dieckmann (dieckmann@iiasa.ac.at)

Approved by

Leen Hordijk
Director, IIASA

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No. 42 Ferrière R, Michod RE: *Wave Patterns in Spatial Games and the Evolution of Cooperation.* IIASA Interim Report IR-99-041 (1999). Dieckmann U, Law R, Metz JAJ (eds): The Geometry of Ecological Interactions: Simplifying Spatial Complexity, Cambridge University Press, Cambridge, UK, pp. 318-332 (2000).

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No. 46 Doebeli M, Dieckmann U: *Evolutionary Branching and Sympatric Speciation Caused by Different Types of Ecological Interactions.* IIASA Interim Report IR-00-040 (2000). The American Naturalist 156:S77-S101 (2000).

No. 47 Heino M, Hanski I: *Evolution of Migration Rate in a Spatially Realistic Metapopulation Model.* IIASA Interim Report IR-00-044 (2000). The American Naturalist 157:495-511 (2001).

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No. 52 Heino M, Laaka-Lindberg S: *Clonal Dynamics and Evolution of Dormancy in the Leafy Hepatic Lophozia Silvicola.* IIASA Interim Report IR-01-018 (2001). Oikos 94:525-532 (2001).

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No. 62 Cheptou P, Dieckmann U: *The Evolution of Self-Fertilization in Density-Regulated Populations .* IIASA Interim Report IR-02-024 (2002). Proceedings of the Royal Society of London Series B 269:1177-1186 (2002).

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No. 65 Dercole F, Ferrière R, Rinaldi S: *Ecological Bistability and Evolutionary Reversals under Asymmetrical Competition.* IIASA Interim Report IR-02-053 (2002). Evolution 56:1081-1090 (2002).

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No. 70 Dercole F, Irisson J, Rinaldi S: *Bifurcation Analysis of a Prey-Predator Coevolution Model.* IIASA Interim Report IR-02-078 (2002). SIAM Journal on Applied Mathematics 63:1378-1391 (2003).

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Adaptive dynamics as a mathematical tool for studying the ecology of speciation processes

Michael Doebeli[1] and Ulf Dieckmann[2]

[1]Department of Zoology and Department of Mathematics, University of British Columbia, Vancouver, BC, Canada
6270 University Boulevard, Vancouver, BC V6T 1Z4, Canada
Email: doebeli@zoology.ubc.ca, phone: +1-604-822-3326

[2]Adaptive Dynamics Network, International Institute for Applied Systems Analysis
A-2361 Laxenburg, Austria
Email: dieckmann@iiasa.ac.at; phone: +43-2236-807-386

After Ernst Mayr published his seminal book in 1963 (Mayr 1963), the issue of speciation appeared to be settled: according to the established dogma, biological diversification occurred in allopatry due to the accumulation of genetic differences in geographically isolated populations. Despite repeated challenges, this view still prevails today, although perhaps less dominantly than before. The earliest rigorous theoretical challenge was provided by Maynard Smith (1966), who produced the first models of speciation in sympatry. These models were based on very simple ecological and genetic assumptions, with two resource types (or niches) and two loci, one for ecological performance and one for mate choice. Despite its simplicity, this type of model has formed the conceptual basis for most of the theory of sympatric speciation that has been developed since then (Kawecki 2004).

For sympatric speciation to occur in sexual populations, two processes must unfold. First, frequency-dependent interactions must generate disruptive selection. Second, a lineage split in sexual populations requires the evolution of assortative mating mechanisms. Skepticism towards the feasibility of both these processes has led to a dismissal of sympatric speciation as a plausible mode of diversification. For example, based on Felsenstein’s (1981) seminal paper, it has long been thought that recombination between traits under disruptive selection and mating traits responsible for assortativeness can be a significant hindrance to the evolution of reproductive isolation between diverging lineages. Similarly, one of the main reasons why the theoretical developments following in the footsteps of Maynard Smith’s model failed to convince speciation researchers was that these models seemed to rely on rather particular ecological circumstances, such as host race formation (Diehl and Bush 1989), and that the ecological conditions for the emergence of disruptive selection in these models were rather restrictive (Kassen 2002, Kawecki 2004).

However, there is another line of thinking about the ecology of speciation that already started – how else could it be? – with Darwin, who concluded:

> "Consequently, I cannot doubt that in the course of many thousands of generations, the most distinct varieties of any one species [...] would always have the best chance of succeeding and of increasing in numbers, and thus of supplanting the less distinct varieties; and varieties, when rendered very distinct from each other, take the rank of species." (Darwin 1859, p. 155)

According to this view, and in modern parlance, frequency-dependent competition between similar ecological types can lead to disruptive selection and diversification. This perspective was embodied in the concept of competitive speciation by Rosenzweig (1978) and further studied by Seger (1985), who presented the first mathematical model showing that frequency-dependent competition for occupation of a niche continuum can induce sympatric speciation under certain conditions. More generally, it was argued by Kondrashov (1986) that frequency-dependent selection on a continuous character can induce bimodal splits in the character distribution, with the two modes representing emerging species. In Kondrashov's models, the disruptive selection regime giving rise to bimodality is simply a consequence of the a priori assumption that the fitness of common types is low, while that of rare types is high. It is difficult to assess the generality of these models, because it is not clear under what conditions ecological interactions would generate such a frequency-dependent selection regime. In fact, it is known that both competitive interactions (Christiansen 1991) and predator-prey interactions (Abrams et al. 1993) can generate evolutionary scenarios in which the population mean of a continuous trait (such as body size) evolves to a state in which selection becomes disruptive. However, somewhat surprisingly, these results were never put into the common context of speciation, perhaps because these studies used the framework of quantitative genetics and thus assumed Gaussian phenotype distributions with constant variances (and hence implicitly assumed random mating).

Overall, it thus remained questionable whether the emergence of disruptive selection due to frequency-dependent interactions would be a general and plausible ecological scenario. In fact, it still seems to be the common wisdom that the origin and maintenance of diversity due to frequency-dependent selection regimes requires a delicate balance of different ecological factors (e.g., Kassen 2002), and that, consequently, most biological diversification occurs in allopatry.

We believe that the advent of adaptive dynamics, and in particular the discovery of the phenomenon of evolutionary branching, will change this perspective fundamentally (Dieckmann et al. 2004). Adaptive dynamics is a general framework for studying evolution of quantitative characters due to frequency-dependent interactions. Within this framework, evolutionary branching points represent potential springboards for sympatric speciation: even though such points are attractors for the adaptive dynamics of a unimodal quantitative trait, populations that have converged on such a point experience frequency-dependent disruptive selection for adaptive and sympatric diversification. Technically speaking, evolutionary branching points are singular points of the adaptive dynamics that satisfy certain general mathematical conditions. The existence and location of such points can readily be investigated in any adaptive dynamics model, following simple and general procedures. Therefore, the concept of evolutionary branching points serves as a unifying principle for investigating the ecological conditions for adaptive diversification and speciation. Using the tools of adaptive dynamics theory, any ecological scenario can be investigated as to its potential for giving rise to diversification, thus rendering obsolete the conceptually isolated and often idiosyncratic analysis of different ecological scenarios.

In fact, it has become clear from numerous studies over the past few years that evolutionary branching points are a robust feature of many different adaptive dynamics models (e.g., Metz et al. 1996, Doebeli and Ruxton 1997, Meszéna et al. 1997, Geritz et al. 1998, Kisdi 1999, Dieckmann and Doebeli 1999, Kisdi and Geritz 1999, Parvinen 1999, Doebeli and Dieckmann 2000, Law et al. 2001, Maire et al. 2001, Van Doorn et al. 2001, Doebeli 2002, Claessen and Dieckmann 2002, Mizera and Meszéna 2003, Doebeli and Dieckmann 2003, Bowers et al. 2003, Van Doorn et al. 2004; for a much more exhaustive list of models of evolutionary branching, readers might wish to consult the following website: www.helsinki.fi/~mgyllenb/addyn.htm). Thus, condensing the ecological conditions for sympatric speciation in the concept of evolutionary branching points supports the insight that the emergence of disruptive selection due to frequency-dependent interactions is an entirely plausible, and in fact ubiquitously applicable evolutionary scenario. To us, this appears to be an important development, which Waxman and Gavrilets (2005) ignored in their discussion of adaptive dynamics in the context of sympatric speciation, thereby essentially claiming that no new advances over previous models can be gained from the unifying perspective of evolutionary branching. This is hard to understand in view of the fact that it is always a goal of the scientific enterprise to find general principles of which any particular scenarios can be seen as special cases.

Instead of recognizing the potentially fruitful role that adaptive dynamics theory can play in providing a general framework for studying the ecological conditions required for sympatric speciation, Waxman and Gavrilets criticize those aspects of recent speciation models that go beyond the clonal theory of adaptive dynamics by addressing the genetic splitting of initially randomly mating sexual populations. As mentioned above, the evolution of assortative mating mechanisms is of course a crucial component of any model of sympatric speciation. In general, one envisages two different scenarios (Kirkpatrick and Ravigne 2002, Dieckmann and Doebeli 2004): with direct assortative mating, assortative mating is based on the character that is under disruptive selection; with indirect assortative mating, assortative mating is based on some ecologically neutral marker traits. In both cases, the degree of assortativeness may be assumed to be either fixed, or may itself be an evolving trait.

With direct assortative mating, a population under frequency-dependent disruptive selection splits into two reproductively isolated subpopulations when the degree of assortativity is (or evolves to be) high enough in the ancestral population. When the degree of assortativeness is an evolving trait, speciation therefore only requires the substitution of one type of alleles, those coding for assortative mating, in the entire population. Models with direct assortative mating thus correspond to the 1-allele models of Felsenstein (1981). It is generally thought that in a population experiencing disruptive selection due to frequency-dependent interactions, speciation will readily ensue with direct assortative mating, because in such populations there is directional selection for higher degrees of direct assortative mating (see also Matessi et al. 2001). With indirect assortative mating, assortativity can only latch on to the ecological trait under disruptive selection if a linkage disequilibrium develops between the ecological trait and the marker trait on which assortative mating is based. Even with a high degree of assortativeness, speciation thus requires the establishment of a polymorphism in the marker trait, and hence the substitution of different alleles in the two emerging subpopulations. Therefore, models with indirect assortative mating correspond to the 2-allele models of Felsenstein (1981). Because of the requirement of a linkage disequilibrium between the marker trait and the ecological trait, it is generally believed that speciation is unlikely to happen with indirect assortative mating.

However, as recent work has shown, such skepticism may often be unwarranted. Both Kondrashov and Kondrashov (1999) and Dieckmann and Doebeli (1999) have demonstrated that, in fact, sympatric speciation can readily occur also with indirect assortative mating. The modeling approaches in these two studies differ: while Dieckmann and Doebeli (1999) allow for the evolution of the degree of assortative mating, Kondrashov and Kondrashov (1999) do not consider such evolution, but instead focus on indirect assortative mating being determined by a preference trait in females and a marker trait in males. Both articles address the basic question of whether indirect assortative mating can lead to speciation in populations experiencing disruptive selection. (Note again that this question is different from the question of how the disruptive selection regime is generated in the first place.) Both papers use models in which all traits involved are determined by many additive loci to show that speciation can, in principle, occur with indirect assortative mating.

Waxman and Gavrilets do not mention the paper by Kondrashov and Kondrashov (1999), but criticize our model in various ways, albeit without backing up their criticisms with results. For example, they suggest that some of the assumptions in Dieckmann and Doebeli (1999) are biologically unjustified. Waxman and Gavrilets venture that our analysis was, strictly speaking, not about sympatric speciation since initial allele frequencies in the illustrations presented in our article were always chosen at ½,. This is far-fetched. First of all, alleles for the ecological trait were not always started at ½ in Dieckmann and Doebeli (1999) (see, e.g., Figure 3 in that paper). Second, for a neutral marker trait the assumption of allele frequencies of ½ in an individual-based model seems actually quite reasonable. Finally, only intermediate values of the assortative mating trait result in random mating, which is a suitable initial condition for studying the evolution of assortative mating. Therefore, allele frequencies of ½ for this trait again seem appropriate here. Nevertheless, to refute the objection, we have explicitly tested the models of Dieckmann and Doebeli (1999) by choosing different initial conditions for the allele frequencies, with the result that, as expected, the evolutionary outcome is just the same (Figure 1a).

Waxman and Gavrilets also assert that the mutation rates in our models are unrealistic. To address this concern, it is helpful to realize that this claim is based on too narrow a perspective on the genetic architecture of ecologically important quantitative traits. Clearly, the view of having, e.g., five independent and freely recombining single loci determining a quantitative trait such as body size is naïve. Instead, in such additive multi-locus models, a 'locus' should be understood not as coding for a single protein, but more generally as describing independent stretches of DNA of variable length which affect the trait under consideration additively, and which recombine freely with other such stretches of DNA. In particular, such stretches might be very much longer than a single locus, and hence the mutation rate per such stretch might be quite high. Another way of seeing this is by realizing that with five diploid loci and a mutation rate of 10^{-3} per locus, the chance of having at least one mutation occurring in an offspring is roughly 10^{-2}. For the population sizes that we used in our models, which range between 500 and 1000, this means that we have, on average, 5-10 mutations in the population per generation. If anything, this seems to be a rather small number for mutations of small additive effects on a quantitative trait. With a per locus mutation rate of 10^{-6} that Waxman and Gavrilets regard as realistic, we would obtain one small additive mutation every 100 generations. To us, such a low number would seem to be very unrealistic indeed.

It is also reassuring that speciation still occurs in the models of Dieckmann and Doebeli (1999) even when the mutation rate is decreased by an order of magnitude (Figure 2). In general, rates of speciation in these models are lower with lower mutation rates, particularly with indirect assortative mating, as in this case speciation relies on the inherently stochastic process of building up a linkage disequilibrium. We note that in principle, this slowing down can be counteracted by any increase in population size, which has to be kept modest in genetically explicit and individual-based numerical explorations for reasons of computational tractability. Based on these considerations, we conclude that the requirements for speciation to occur in these models are not biologically unrealistic.

Finally, Waxman and Gavrilets note that our models do not include costs of assortativeness, and that such costs would likely impede the speciation process. This point is as correct as it is obvious: of course one must expect large costs of assortative mating to preclude evolution of assortative mating. Consequently, the actual question is not so much whether or not speciation occurs when such costs are present, but rather whether or not the threshold costs predicted by the models are unreasonably low compared with natural settings. By extending the models by Dieckmann and Doebeli (1999) to include costs of assortative mating we can see that the evolution of assortative mating remains possible even when such costs are substantial. There are various ways in which one can introduce these costs into our models, and Figure 3 illustrates two cases.

In the first case, costs depend on the current distribution of the assortative mating trait in the population, so that the most assortative female in the population has a cost c (incurred as a reduction of her fecundity) compared with the least assortative female. Thus, whenever mating takes place, the chance of reproducing is $1 - c$ for the female with the highest degree of choosiness, while the female with the least degree of choosiness mates with certainty, with the mating chances of other females varying linearly in between. The cost that a particular degree of assortativeness implies therefore depends on how assortative other females in the population are, reflecting a scenario in which it is the relative choosiness of females that determines their chances of producing offspring.

Alternatively, costs of assortativeness can be incorporated by granting only a finite number of N sequential mate-choice trials to females that have the opportunity to reproduce (see e.g., Matessi et al. 2001, Arnegard and Kondrashov 2004). In each such trial, a potential mate is first randomly selected from the population and, depending on the female’s choosiness and preference, is then either rejected or accepted. In the latter case, the female reproduces. If a female rejects all N potential mates during a given mating opportunity, she cannot reproduce and has to wait until her next opportunity to reproduce comes up at a later moment, at which time she initiates a new round of mate-choice trials. The chance that a female will not accept any of the N potential mates depends on her choosiness, i.e., on her degree of assortativeness, and on the frequency of acceptable mates in the population. Moreover, as the number of allowed mate-choice trials N decreases, the chance increases that females with a given degree of assortativity reject all N males. Hence the cost of assortativeness rises with increasing female choosiness, with a decreasing frequency of acceptable mates, and with a decreasing number of allowed mate-choice trials.

Figure 3 shows scenarios in which speciation occurs despite these two types of costs, both for direct and indirect assortative mating. Again, as expected, costs are more effective in preventing speciation under indirect assortative mating. Yet, it is difficult to assess what constitutes large costs. For example, $N = 200$ used in Figure 3d might seem a rather large number of mate-choice trials, and hence to represent a small cost. However, in natural populations mate-choice trials may actually be based on very brief and fleeting encounters (involving e.g., only visual inspection). Thus, $N = 200$ may actually be rather small, representing a substantial cost. For instance, in a band of chimpanzees, as well as in humans of certain age classes, individuals may have hundreds of mate-choice trials, evaluating the suitability of potential mates before reproducing. It should also be borne in mind that individuals in many species are bound to reduce their choosiness when encountering a low frequency of suitable mates. Such plasticity reduces the costs of assortative mating and thus facilitates speciation in the models considered here. After all, fully random mating appears to be rare in nature, which suggests that costs of assortativeness are not typically very large.

Of course, the issues discussed above will still benefit from a more systematic analysis. For example, Doebeli (2005) investigates the effects of costs of assortative mating in a variant of the models used here. The examples given in Figure 3 already show that in the models of Dieckmann and Doebeli (1999), speciation is robust to introducing costs of assortative mating as long as these costs are not too large. The flip side of this statement, that mating costs can be increased to levels at which the evolution of assortative mating is obstructed, seems to be a truism. It is also intuitively clear that costs of assortative mating are bound to slow down the speciation process, as has already been noted by Kirkpatrick and Nuismer (2004) and by Bolnick (2004). Bolnick (2004), whose models are based on Dieckmann and Doebeli (1999) (see also Bolnick and Doebeli 2003), strikes a rather cautionary note, but it is clear from Figures 2 and 3 in his paper that speciation still occurs within reasonable time frames for a large range of model parameters. We certainly agree with Bolnick (2004) that it will be fruitful to investigate relevant parameter regions in natural systems.

The assortative mating models of Dieckmann and Doebeli (1999), as well as those of Kondrashov and Kondrashov (1999), must by no means be perceived as being the last word on the topic. We recommend that these models should rather be viewed as a starting point for re-evaluating the view that recombination between ecological traits under disruptive selection and mating traits responsible for reproductive isolation prevents sympatric speciation. To proceed with this re-evaluation, different mating models need to be considered, e.g., models that investigate the evolution of the degree of assortative mating when mating is determined by a preference trait in females and a marker trait in males. In this case, speciation is hindered not only by recombination between ecological traits and mating traits, but also by recombination among mating traits, i.e., between loci coding for the female preference and the male marker trait. Doebeli (2005) reports that speciation is still feasible in such models, a result that holds even when there are costs of assortative mating. In addition, it is important to consider models that explore the possibility of sympatric speciation being driven by sexual selection alone, i.e., by selection resulting from differential mating success (see Van Doorn et al. 2004 and Arnegard and Kondrashov 2004 for two recent studies on this topic). We agree with Waxman and Gavrilets that there is quite some room for exploring effects of costs of assortative mating on the dynamics of speciation models. However, it is already clear from the models available to date that the evolution of assortative mating mechanisms can, in theory and under biologically reasonable assumptions, lead to reproductive isolation between subpopulations emerging in an ancestral population under disruptive selection, even in the presence of such costs. It is also clear that requirements for speciation are more stringent with indirect assortative mating than with direct assortative mating, but even with indirect assortative mating speciation does not seem to be a theoretically unlikely process.

Thus, perhaps the more fundamental issue – and certainly one of central relevance – is whether regimes of disruptive selection due to frequency-dependent ecological interactions are common or rare in nature. On the theoretical side, the framework of adaptive dynamics is able to provide a clear answer: evolutionary branching points are a common feature of adaptive dynamics models, and this conclusion has been shown to extend to a great variety of different types of ecological scenarios. In general, populations that are attracted by evolutionary branching points remain there until rescued evolutionarily by mechanisms, such as assortative mating, that allow for an escape from the underlying fitness minima. While it remains to be seen whether sympatric speciation is indeed much more common in natural systems than was previously believed, adaptive dynamics theory has already now provided new perspectives for empirical studies of the ecology of speciation, e.g., for investigations of tractably rapid diversification in microorganisms (Rainey and Travisano 1998, Travisano and Rainey 2000, Kassen 2002, Friesen et al. 2004).

References

Abrams, P. A., Matsuda, H. and Harada, Y. 1993. Evolutionarily unstable fitness maxima and stable fitness minima of continuous traits. *Evolutionary Ecology* **7**: 465-487.

Arnegard, M. E. and Kondrashov, A. S. Sympatric speciation by sexual selection alone is unlikely. *Evolution* **58**: 222-237.

Bolnick, D.I. 2004. Waiting for sympatric speciation. *Evolution* **58**: 895-899.

Bolnick, D. and Doebeli, M. 2003. Sexual dimorphism and adaptive speciation: two sides of the same ecological coin. *Evolution* **57**, 2433–2449.

Bowers RG, White A, Boots M, Geritz SAH, Kisdi E. 2003. Evolutionary branching/speciation: contrasting results from systems with explicit or emergent carrying capacities. *Evolutionary Ecology Research* **5**: 883-891.

Christiansen, F. B. 1991. On conditions for evolutionary stability for a continuously varying trait. *Theoretical Population Biology* **7**: 13-38.

Claessen, D. and Dieckmann, U. 2002. Ontogenetic niche shifts and evolutionary branching in size-structured populations. *Evolutionary Ecology Research* **4**: 189-217.

Darwin, C. 1859. *On the Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Lif*e. Reprinted 1964. Cambridge, MA, USA: Harvard University Press.

Dieckmann, U. and Doebeli, M. 1999. On the origin of species by sympatric speciation. *Nature* **400**: 354-357.

Dieckmann, U. and Doebeli, M. 2004. Adaptive dynamics of speciation: Sexual populations. pp. 76-111 *in* U. Dieckmann, M. Doebeli, J.A.J. Metz and D. Tautz, eds. *Adaptive Speciation*. Cambridge University Press, Cambridge, UK.

Dieckmann, U., Doebeli, M., Metz, J.A.J. and Tautz, D. (eds.) 2004. *Adaptive Speciation*. Cambridge University Press, Cambridge, UK.

Diehl, S. R., and Bush, G. L. 1989. The role of habitat preference in adaptation and speciation. pp. 345-365 *in* D. Otte and J. Endler, eds. *Speciation and its consequences.* Sinauer Associates, Sunderland, MA.

Doebeli, M. 2002. A model for the evolutionary dynamics of cross-feeding polymorphisms in microorganisms. *Population Ecology* **44**: 59-70.

Doebeli, M. 2005. Adaptive speciation when assortative mating is based on female preference for male marker traits, Journal of Evolutionary Biology (in press).

Doebeli, M. and Ruxton, G.D. 1997. Evolution of dispersal rates in metapopulation models: Branching and cyclic dynamics in phenotype space. *Evolution* **51**: 1730-1741.

Doebeli, M. and Dieckmann, U. 2000. Evolutionary branching and sympatric speciation caused by different types of ecological interactions. *The American Naturalist* **156**: S77-S101.

Doebeli, M, and Dieckmann, U. 2003. Speciation along environmental gradients *Nature* **421**: 259-264.

Felsenstein, J. 1981. Skepticism towards Santa Rosalia, or why are there so few kinds of animals? *Evolution* **35**: 124-238.

Friesen, M., Saxer, G., Travisano, M. and Doebeli, M. 2004. Experimental evidence for sympatric ecological diversification due to frequency-dependent competition in *Escherichia coli.* *Evolution* **58**: 245-260.

Geritz, S.A.H., Kisdi, É., Meszéna, G. and Metz, J.A.J. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology Research* **12**: 35-57.

Kassen, R. 2002. The experimental evolution of specialists, generalists, and the maintenance of diversity. *Journal of Evolutionary Biology* **15**: 173-190.

Kawecki, T. J. 2004. Genetic theories of sympatric speciation. pp. 36-53 *in* U. Dieckmann, M. Doebeli, J.A.J. Metz and D. Tautz, eds. *Adaptive Speciation*. Cambridge University Press, Cambridge, UK.

Kirkpatrick, M. and Ravigné, V. 2002 Speciation by natural and sexual selection: models and experiments. *American Naturalist* **159**: S22-S35.

Kirkpatrick M. and Nuismer, S.L., 2004. Sexual selection can constrain sympatric speciation. *Proc. Roy. Soc. B* **271**: 687-693.

Kisdi, É. 1999. Evolutionary branching under asymmetric competition. *Journal of Theoretical Biology* **197**: 149-162.

Kisdi, É. and Geritz, S.A.H. 1999. Adaptive dynamics in allele space: Evolution of genetic polymorphism by small mutations in a heterogeneous environment. *Evolution* **53**: 993-1008.

Kondrashov, A.S. 1986. Multilocus model of sympatric speciation. III. Computer simulations. *Theoretical Population Biology* **29**: 1-15.

Kondrashov, A.S. and Kondrashov, F.A. 1999. Interactions among quantitative traits in the course of sympatric speciation. *Nature* **400**: 351-354.

Law, R., Bronstein, J.L. and Ferrière, R. 2001. On mutualists and exploiters: Plant-insect coevolution in pollinating seed-parasite systems. *Journal of Theoretical Biology* **212**: 373-389.

Maire, N., Ackermann, M. Doebeli, M. 2001. On the evolution of anisogamy through evolutionary branching. *Selection* 2: 107-119.

Matessi, C., Gimelfarb, A. and Gavrilets, S. 2001. Long-term buildup of reproductive isolation promoted by disruptive selection: How far does it go? *Selection* **2**: 41-64.

Maynard Smith, J. 1966. Sympatric speciation. *The American Naturalist* **100**: 637-650.

Mayr, E. 1963. *Animal Species and Evolution*. Cambridge, MA, USA: Harvard University Press.

Meszéna, G., Czibula, I. and Geritz, S.A.H. 1997. Adaptive dynamics in a 2-patch environment: A toy model for allopatric and parapatric speciation. *Journal of Biological Systems* **5**: 265-284.

Metz, J.A.J., Geritz, S.A.H., Meszéna, G., Jacobs, F.J.A. and van Heerwaarden, J.S. 1996. Adaptive dynamics: A geometrical study of the consequences of nearly faithful reproduction. pp. 183-231 *in* van Strien, S.J. and Verduyn Lunel, S.M., eds. *Stochastic and Spatial Structures of Dynamical Systems, Proceedings of the Royal Dutch Academy of Science (KNAW Verhandelingen)*. Dordrecht, Netherlands: North Holland.

Mizera, F. and Meszéna, G. (2003). Spatial niche packing, character displacement and adaptive speciation along an environmental gradient. *Evolutionary Ecology Research* **5**: 363-382.

Rainey, P.B. and Travisano, M. 1998. Adaptive radiation in a heterogeneous environment. *Nature* **394**: 69-72.

Rosenzweig, M.L. 1978. Competitive speciation. *Biological Journal of the Linnean Society* **10**: 275-289.

Seger, J. 1985. Intraspecific resource competition as a cause of sympatric speciation. In *Evolution: Essays in Honour of John Maynard Smith*, eds. Greenwood, P.J., Harvey, P.H. and Slatkin, M., pp. 43-53, Cambridge University Press, Cambridge.

Parvinen, K. 1999. Evolutionary branching of dispersal strategies in structured metapopulations. *Journal of Mathematical Biology* **45**: 106-124.

Travisano, M. and Rainey, P.B. 2000. Studies of adaptive radiation using model microbial systems. *The American Naturalist* **156**: S35-S44.

Van Doorn, G.S., Dieckmann, U. and Weissing, F.J. 2004. Sympatric speciation by sexual selection: A critical re-evaluation. *The American Naturalist* 163, 709-725.

Van Doorn, G.S., Luttikhuizen, P.C. and Weissing, F.J. 2001. Sexual selection at the protein level drives the extraordinary divergence of sex related genes during sympatric speciation. *Proceedings of the Royal Society of London B* **268**: 2155-2161.

Waxman, D., and Gavrilets, S. 2005. 20 Questions on Adaptive Dynamics. *Journal of Evolutionary Biology*, in press.

Figure legends

Fig. 1 Adaptive speciation in the model of Dieckmann and Doebeli (1999) for different initial conditions. (a) Direct assortative mating; (b) Indirect assortative mating. Individual genomes were initialized by assuming that for each trait, the first of 5 diploid loci was fixed for the 1-allele, while the other loci were fixed for the 0 allele. In (a), the lower panel shows the evolution of the degree of assortative mating (mating character). In (b) the lower panels show the evolution of this degree and of the marker character. When speciation occurs with indirect assortative mating, each of the two marker clusters rapidly develops into complete linkage disequilibrium with one of the two ecological clusters. The setup of the shown individual-based simulations is described in Dieckmann and Doebeli (1999). Parameters: $c_K = 2.0$, $c_\alpha = 0.6$ in (a); $c_K = 2.0$, $c_\alpha = 0.3$ in (b).

Fig. 2 Adaptive speciation in the model of Dieckmann and Doebeli (1999) for lower mutation rates. (a) Direct assortative mating; (b) Indirect assortative mating. Panel organization as in Figure 1. The per locus mutation rate was set to 10^{-4}. Other parameters as in Fig. 1a for (a), and as in Fig. 1b for (b); initial conditions as in Dieckmann and Doebeli (1999).

Fig. 3 Adaptive speciation in the model of Dieckmann and Doebeli (1999) with costs of assortative mating. (a) Direct assortative mating with a frequency-dependent cost c = 0.35, such that whenever mating takes place, the chance of reproducing for the female that encounters the least amount of suitable partners is 1-c, while the female that encounters the highest amount of suitable partners mates with certainty. In between, females have intermediate chances of mating and reproducing (obtained through linear interpolation between the two extremal values 1-c and 1). (b) Direct assortative mating with finitely many mate-choice trials, $N = 20$. (c) Same as (a), but with indirect assortative mating and $c = 0.15$. (d) Same as (b), but with indirect assortative mating and $N = 200$. Other parameters as in Fig. 2a for (a) and (b), and as in Fig. 2b for (c) and (d). In all cases, only the time series of the ecological character is shown; if assortative mating is direct, as in (a) and b), the time series of the mating character are similar to those shown in Figures 1a and 2a; if assortative mating is indirect, as in (c) and (d), the time series of the mating characters are similar to those shown in Figures 1b and 2b.

Figure 1, Doebeli & Dieckmann

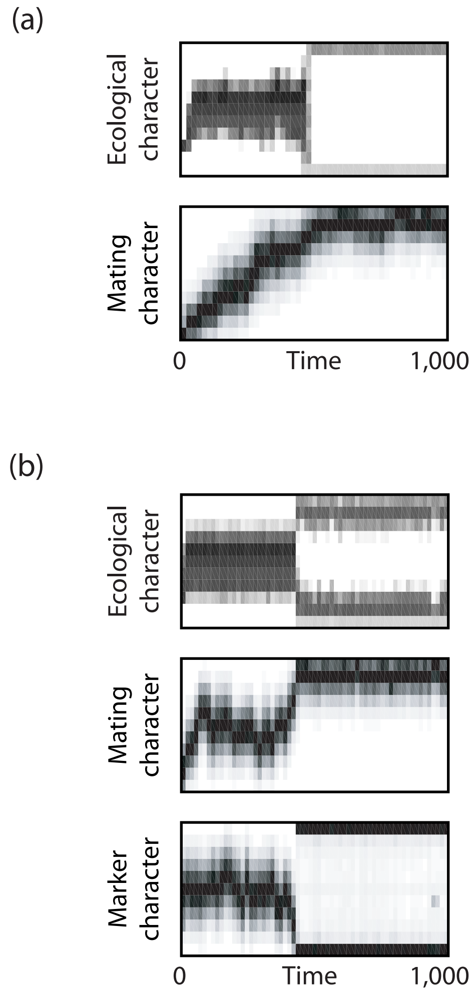

Figure 2, Doebeli & Dieckmann

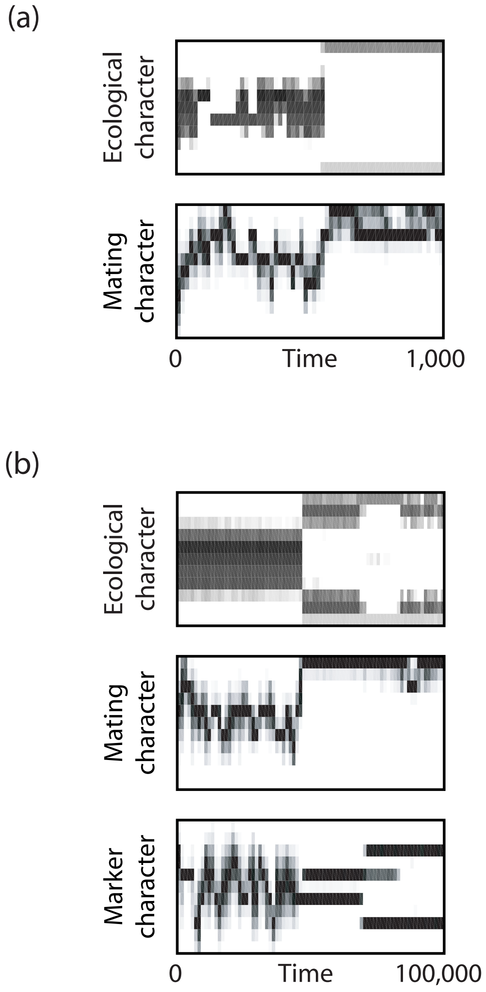

Figure 3, Doebeli & Dieckmann