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COMMENTARY

The way the world might be

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Theoreticians are interested in the way the world might be, seeking theories of 'elegant and economical…mathematical form, in the expectation that they will prove the ones realized in nature' (Polkinghorne, 1983, p. 9–10). Empiricists, on the contrary, prefer to know 'The Way the World Is' (as in Polkinghorne's title). Ideally, our understanding advances by an interplay between the two. As Darwin insisted 'all observation must be for or against some view if it is to be of any service!' (see Browne, 2002, p. 56): gathering of experimental and observational data without a guiding theoretical framework is generally not productive. A good guide to the value of new theory, therefore, should be its impact on the course of empirical work and, conversely, new theory should be firmly grounded in the existing body of data.

How does Adaptive Dynamics fare in this context? We were struck by the fact that Waxman & Gavrilets' (2004) review contains only a single reference to an empirical study amongst its 90 or so citations. They are critical of the Adaptive Dynamics approach primarily on theoretical grounds, challenging one view of how the world might be with other views of how it might be, rather than confronting the theory with the way the world actually is. The empiricist encountering Waxman and Gavrilets' Section 4 on the major assumptions of Adaptive Dynamics might have expected to see these assumptions compared with data. There are data available on the sizes of allelic effects and on the numbers of loci contributing to standing genetic variation (e.g. Hayes & Goddard, 2001; Mackay, 2001) or the differences between species in quantitative traits (Orr, 2001), on the prevalence of dominance and epistasis (e.g. Lukens & Doebley, 1999) and on effective population sizes (and hence drift) (e.g. Frankham, 1995). The Adaptive Dynamics assumptions do not fit easily into this body of information: genetic variation in quantitative traits within populations is almost ubiquitous, mutations of large effect do occur with appreciable frequency, departures from additivity are widespread and effective population sizes are often small.

Of course, models must make simplifying assumptions, so how do we judge what Waxman and Gavrilets call 'the consequences of violation'? Surely, the answer must be to compare the predictions of models with empirical observations. Ideally, one would do this in simple and well-understood situations before going on to make predictions about more complex problems where discrepancies may have many different explanations (like sympatric speciation, see below). Population genetics theory provides good predictions of the outcome of both selection and drift in controlled laboratory experiments and simple natural situations, like the evolution of insecticide resistance (Taylor, 1986). The same is true for game theory (e.g. dung fly waiting times: Parker, 1970). Can similar tests be devised for Adaptive Dynamics? We strongly support the call by Waxman and Gavrilets (Section 6) for comparisons between model predictions and empirical data but we see no clear guidance for empiricists on the critical data they need to collect, either in the Adaptive Dynamics literature or in Waxman and Gavrilets' review.

Adaptive Dynamics came to the attention of many evolutionary biologists through the sympatric speciation model of Dieckmann & Doebeli (1999) (hereafter DD99). Waxman and Gavrilets are critical of this contribution on several counts (Sections 5.2 & 5.3). Whatever the merits of these arguments, it is clear that a complex model, building on a long history of theoretical development and claiming to arrive at a different conclusion, should not be accepted without careful examination. We have investigated the impact of DD99 on views of sympatric speciation as an example of the interplay between theoretical and empirical approaches in evolutionary biology.

A search of the ISI Science Citation Index (Expanded) on 5 April 2004 revealed 200 citations of DD99. The original paper was published in a well-known weekly magazine, *Nature*, whose extremely condensed format makes it very difficult to provide adequate detail, for example about the assumptions inherent in a simulation model. Dieckmann and Doebeli expanded their arguments and provided a more extensive discussion in a subsequent paper (Doebeli & Dieckmann, 2000) but this has only been cited 39 times. Abrams (2001) compared the Adaptive Dynamics approach with population genetic and game theory approaches. He questioned the assumption in DD99 that there is no cost to assortative mating and considered the effectiveness of mate selection in the model to be unrealistically high. Abrams' paper has been cited only 12 times. Similarly, Day (2001) pointed out that population structure reduces the tendency towards evolutionary branching and is absent in the DD99 model. Waxman and Gavrilets note the ubiquity of population structure (Section 5.3), although they draw different implications. Day's paper has been cited only three times compared with over 100 citations in the same time post-publication for DD99.

We classified papers citing DD99 according to the type of contribution (empirical, theoretical or review/comment) and on whether nonallopatric speciation was a central issue in the paper or not (Table 1). We then looked at the way DD99 was reported: was it quoted as evidence that nonallopatric speciation is now considered

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Table 1 Analysis of papers citing Dieckmann & Doebeli, 1999.

Type of paper	Nonallopatric speciation a major part of the subject matter	Use of DD99 reference in respect of the likelihood of nonallopatric speciation		Papers discussing content of DD99 and/or querying assumptions or conclusions	
		No change	Positive	No change	Positive
Empirical	Yes	22	32	1	0
	No	18	9	0	0
Theoretical	Yes	19	11	4	2
	No	24	0	2	0
Review or comment	Yes	11	15	2	1
	No	16	6	1	0
Excluded	Not available 12	Dieckmann or Doebeli amongst authors 5			

more likely, rapid, or plausible under a wide range of conditions ('positive' in Table 1), or simply as indicating that sympatric speciation is possible without a particular change in view ('no change'). We found no papers using DD99 to indicate a negative trend. Finally, we considered whether the paper simply used DD99 to support a statement about nonallopatric speciation, or a related issue, perhaps with a brief description of their model, as opposed to discussing the model in more detail and considering its assumptions or implications.

DD99 is cited in a diverse literature, sometimes for purely methodological reasons and often in papers that make only passing reference to speciation. In these papers, the references are typically neutral (79%). Many use DD99 alone, or in combination with Kondrashov & Kondrashov (1999), as their sole reference to the literature on sympatric speciation. If the function of a reference in such a situation is to provide an entry to the literature for the uninitiated reader, this is probably not ideal: competitive speciation is only one form of sympatric speciation, the treatment in these papers is one-sided, and they provide only limited guidance on the earlier literature. A recent review, such as Via (2001), would be more helpful.

Empirical papers related to nonallopatric speciation frequently cite DD99 in support of positive statements (59%). They very rarely qualify these statements with any discussion of the model or its limitations, although they are often discussing situations far removed from the DD99 scenario. Here are some examples of statements supported by reference to DD99:

'[DD99] showed that sympatric speciation is a likely outcome of competition for resources' Simkova *et al.* (2002).

'[DD99] clearly shows that disruptive selection…may lead to eventual reproductive isolation' Taylor *et al.* (2001).

'the credibility of [sympatric speciation] has recently been greatly strengthened by both theoretical and empirical data' Parker *et al.* (2001).

'[sympatric speciation has] become much more acceptable thanks to recent models' Jocque (2002).

'[DD99] recently presented theoretical evidence that assortative mating often leads to reproductive isolation between ecologically diverging sub-populations which in turn can lead to sympatric speciation' Flier *et al.* (2001).

'sympatric host race formation can occur over a wide range of conditions' Pappers *et al.* (2002).

'sympatric mechanisms [of speciation]…now seem to be both natural and widespread' Stewart (2003).

'[DD99] demonstrate that competition for resources is sufficient for sympatric speciation' Albertson *et al.* (2003).

'the combination of reality and generality strongly supports the interpretation that diverse sympatric sets of related taxa and ecological forms have resulted from divergence in sympatry' Savolainen & Vepsalainen (2003).

'sympatric speciation is possible and may be more common than previously thought' Jones *et al.* (2003).

'resulting in speciation in as few as 300 generations' Wilson *et al.* (2000).

'sympatric speciation is plausible under realistic conditions of ecology and population genetic variation' Shaw *et al.* (2000).

'competition driven speciation is likely to occur rapidly and under a wide range of biologically plausible conditions' Bridle & Jiggins (2000).

There seems to be a widespread and uncritical acceptance of the conclusions of DD99 and, more worrying, an extension to a general view that theoretical objections to sympatric speciation, by whatever mode, suddenly have less force.

Of course, uncritical acceptance is not universal. Mallet and his co-workers, for example, refer to DD99 explicitly as evidence that assortative mating due to pleiotropic effects of selected traits evolves more readily than mate choice based on independent traits (Emelianov *et al.*, 2001; Jiggins *et al.*, 2001; Dres & Mallet, 2002). Theoretical and review papers more often dissect features of the models (27 and 15%, respectively). Theoretical papers are also much less likely to suggest that DD99 necessitates a significant shift in attitude towards nonallopatric speciation (37% amongst those where nonallopatric speciation is a central topic). Typically, it is viewed as part of a continuum of models. Only three of 11 papers in which the model is discussed fall into our 'positive' category: this is because the basic conclusion of DD99 that resource competition *can* lead to sympatric speciation was firmly established before 1999 and these authors are more cautious about whether the DD99 results establish a greater probability, wider range of conditions or more rapid speciation than previous models (Fig. 1).

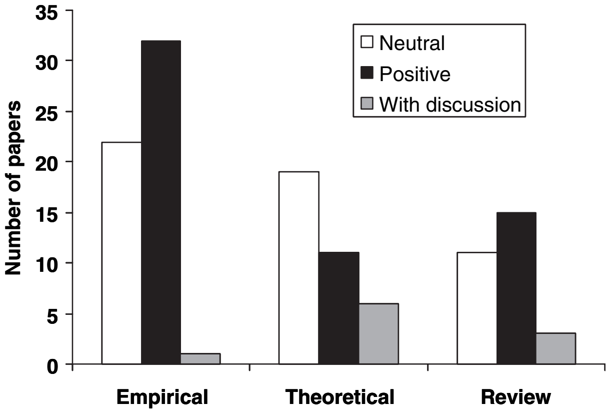

Fig. 1 Analysis of papers citing Dieckmann & Doebeli (1999) in which nonallopatric speciation was a central topic.

Sympatric speciation theory is a case study of a worrying trend in evolutionary biology. Powered by computing, theoreticians are churning out increasingly complex and recondite models that may be impossible to thoroughly describe in a short article, and which require so much effort from the average reader that they may only be fully understood by a handful of people. This problem is compounded by the fact that there is an inevitable citation and (almost certainly) publication bias that favours models that 'show something'. Had DD99 come to the conclusion that sympatric speciation did not occur under realistic assumptions, it is unlikely it would have been published in *Nature*.

This creates pressure on theoreticians to devise approaches that allow interesting things to happen, perhaps resulting in models that are based on unrealistic assumptions. This is not particularly problematic where the models are straightforward, such as the earlier contributions to sympatric speciation theory of Turner & Burrows (1995) and Higashi *et al.* (1999) but, increasingly, models require such an investment in order to be understood by nonspecialists that many empiricists feel they have little option but to read the conclusions and trust that they are objective and relevant.

It is tempting to speculate that the interplay between theoretical and empirical approaches has a characteristic life history. Initial observations stimulate the development of theories that are accessible and testable and provide an essential framework for the development of the field. The complexity of models then increases more rapidly than empiricists can provide the data needed to guide assumptions or test predictions. The modelling side takes on an independent existence where there is no longer great pressure for models to be testable, debate about the models becomes purely theoretical and empiricists either lose interest or simply select models whose output fits their preconceptions. It is easy to find empiricists who view much of the theory in their field as inaccessible and divorced from reality.

We note than none of the nearly 200 papers we examined has set out to test a prediction made by the DD99 model. This brings us back to our starting point: there has to be a constructive interplay between theory and experiment. Theoreticians need to clarify their assumptions so that they can be challenged with observations, and they need to develop models that make discriminating predictions that are accessible to empirical testing. Practical biologists must also do their bit: they must make the effort to read theoretical contributions with the same critical eye that they apply to experimental data, rather than accepting conclusions too readily. Sadly, we feel that the healthy relationship that is usually a strength of evolutionary biology has broken down in this particular case.

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