

THE CONCEPT OF EFFECTIVE RECOMBINATION RATE AND ITS APPLICATION IN SPECIATION THEORY

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The goal of this study is to develop a unifying theoretical framework to quantify the strength of reproductive isolation. We propose the use of the "effective recombination rate," which measures how fast associations of genes are broken by interlocus recombination. Applying the well-established theory of the effective migration rate, we derive two techniques to investigate the effective recombination rate in models of speciation: the weak migration approximation for parapatric scenarios and the weak recombination approximation for sympatric scenarios. We illustrate the use of these two methods by two examples each: (1) single-locus genetic incompatibility and (2) two-locus genetic incompatibility for the first method, and (3) assortative mating and (4) assortative mating combined with disruptive selection for the second method. An advantage of the effective recombination rate over previous approaches is that it integrates gene flow in both directions into a single index measuring the strength of isolation. This enables straightforward comparisons of speciation scenarios with the same or different geographic histories. The method also allows us to evaluate the relative contributions of F2 hybrid deficiency or linkage between multiple barriers in reproductive isolation.

KEY WORDS: Effective migration rate, gene flow, isolating barrier, linkage disequilibrium, reproductive value.

Speciation is one of the fundamental evolutionary puzzles that Darwin essentially failed to address in the *Origin of Species* despite the title of the book. Not to mention empirical researchers (Coyne and Orr 2004; Widmer et al. 2009), this challenging problem intrigued many theoreticians (Turelli et al. 2001; Gavrillets 2004). They contributed numerous mathematical and simulation models, which revealed how species can diverge through various evolutionary mechanisms (Gavrillets 2003, 2004; Dieckmann et al. 2004). Speciation models are still increasing in number, continuously bringing novel ideas and renewing our understanding (e.g., Proulx and Servodio 2009; Barton and de Cara 2009; van Doorn et al. 2009). A consequence of this growth is "balkaniza-

tion" of the subject (Kirkpatrick and Ravigne 2002), which makes synthetic and unifying work important. A major problem in synthesis is, however, that many of the modeling studies focus on conditions for speciation to occur. Given the inherent complexity of speciation, it is usually difficult to extract analytical conditions for speciation from realistic models. Therefore, modelers often use computer simulations with limited parameter values. This makes comparisons between different studies difficult or impossible. Thus, it is an important question what aspect of speciation, if not "occurrence," we can focus on to get a more synthetic view.

We would like to direct attention to consequences of, rather than conditions for, reproductive isolation and speciation, that is,

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