

What can reproductive barriers tell us about speciation?

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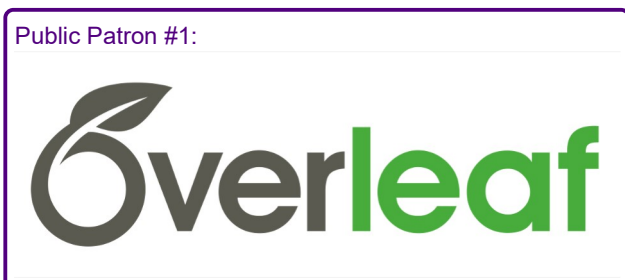
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Introduction

The study of Veen et al. (2013) compares reproductive barriers between species of true crickets (Gryllidae) to evaluate how common multiple barriers are within this clade, and whether or not similar combinations of barriers can cause reproductive isolation. Clade wide information about the absence or presence of reproductive barriers between species is further used to gauge possible routes of speciation. The link between reproductive barriers and routes of speciation is an indirect one, however, the authors argue that if systematic patterns in the presence or absence of barriers between sister taxa can be detected, that they can inform (to some extent) about the processes that have led to the splitting of a species. For example, following the framework laid out in the study, one might expect that if costly hybridisation has led to reinforcement to complete speciation,

then high divergence in prezygotic barriers between the sister species should be detected.

To investigate the relationship between reproductive barriers and speciation Veen et al. (2013) combine two approaches: First, different experiments are employed to detect and quantify pre- and postzygotic barriers between two closely related and hybridizing field crickets, *Gryllus bimaculatus* and *G. campestris*. Second, Veen et al. (2013) conduct an exhaustive review of the literature in the family Gryllidae to compile a summary table with information of reproductive barriers present in other gryllid species. Data from the experiments and the literature survey were subsequently combined to search for patterns in the reproductive barriers present or absent between species pairs.

Merits

The study investigates a core question in evolutionary biology, namely, what are the processes leading to the cessation of gene flow between coexisting individuals. Shedding light on these processes does not only elucidate how individuals become reproductively isolated from one another, but also allows insights into the mechanisms of coexistence and patterns of species diversity. The work by Veen et al. (2013) is both impressive and important in that it compiles a large dataset on the reproductive barriers acting in gryllids, and with that they have provided the most comprehensive overview on reproductive barriers in this family to date.

Studies such as this fill an important gap in speciation studies because the compilation of large cross species datasets allows the detection of general patterns. Finding common patterns across species is of utmost importance and has been highlighted as a major research priority by the Marie Curie Speciation Network (2012).

Critique

The first version of the manuscript provided a solid introduction into the gryllid study system and the underlying questions. However, the length of the Introduction and Methods were overly long due to repetition. Similar comments were made by the other three reviewers, all of them asking for a shorter and more concise manuscript. Furthermore, the introduction did not clearly lay out how this study can advance our understanding of how knowledge about the kinds of reproductive barriers acting between species may elucidate processes that have led to speciation between them. Upon reading the overlapping comments of the reviewers, the authors reduced the overall length of the manuscript and narrowed the framework of the manuscript by focussing more explicitly on reproductive isolation and barriers and their connection to speciation in the revised version of the manuscript.

In my peer review report, I asked the authors (Veen et al. 2013) why they excluded reproductive isolation barriers that affect many species in nature, most notably, temporal isolation and habitat isolation (Dobzhansky 1937; Mayr 1970). These two isolating barriers produce opportunity isolation, which occurs whenever populations have unequal probabilities of encountering one another during the breeding season. For example, opportunity isolation occurs when populations breed at different times (temporal isolation) or when individuals have decreased opportunities to mate because they are separated by a geographic barrier, or have different preferences for breeding habitat (habitat isolation). In the methods of the manuscript, the allopatric distribution of the gryllid sister pair is described eastern Europe and large parts of France and Spain for *C. campestris*, and the region around the Mediterranean for *G. bimaculatus*). These species are found sympatrically in south-eastern Spain. From the distribution data that the authors describe in their manuscript, they could have estimated the degree of spatial overlap between the species on a large scale, which would give a proxy for the potential of species interactions, such as hybridisation or mate competition, throughout their area. Such data may further be used to evaluate the likelihood of a role for vicariance in species divergence. Furthermore, field estimates of fine scale habitat associations could be used to estimate habitat preferences of each species to establish whether fine scale preferences could further contribute to a reduction in encounter probability within the same spatial area. Similarly, temporal isolation between the species may be estimated from phenological data of the species reproductive times, such as the timing and length of the reproductive period. The authors wrote in their reply that they felt that analysing these distribution data or including any other measures of temporal and spatial isolation barriers was beyond the scope of their study. The importance of temporal and habitat isolation was, however, acknowledged.

Lastly, I commented in my peer review report, that their (Veen et al. 2013) presentation of results does not allow for a direct comparison of the strength of different barriers to reproduction, nor did it allow a comparison with other studies. To overcome these limitations, I suggested to use the multiplicative function of individual components of isolation in sequential stages of mating following the methods published in Coyne and Orr (1989; 1997) and Ramsey et al. (2003). This method quantifies the relative contribution of each individual barrier to the total reproductive isolation. In addition, I suggested organizing the results in a way that would make it easier for the reader to get an summary and overview of them. Specifically, I suggested the authors could include an overview in the results on the strength of reproductive barriers. The authors followed my suggestion and included the strength of each barrier and assessed the absolute contribution of each barrier in the revised version of the manuscript. An overview figure summarizing the barriers acting between the gryllid species was also added.

Discussion

The authors state that their results may give important clues regarding the processes leading to speciation in gryllids. But how can it ever be known which (present day) reproductive barriers led to speciation, and which ones accumulated after speciation was completed? This was pointed out by myself and other reviewers, and it was suggested that Veen et al. (2013) more strongly emphasize the limitations of using extant reproductive barriers to infer historical speciation events. The revision of the manuscript incorporated our concerns and the limitation of the framework was more clearly spelt out in the discussion. In particular, the authors more visibly lay out the assumptions of their approach, that is, the assumption that past reproductive barriers may qualitatively persist even over long time scales, although they may decrease in strength. Following this assumption, the consistent lack or presence of some types of reproductive barriers may indeed be used as a diagnostic tool to detect some general trends in speciation pathways.

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