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Speciation is unlikely to drive divergence rates

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In our recent *TREE* review [1], we argue that the term ‘punctuated equilibrium’ (PE) is an umbrella term that encapsulates a number of conceptually distinct ideas and that conflating these has led to unnecessary confusion and hindered progress in addressing macroevolutionary questions. In a letter written in response to our paper, Venditti and Pagel [2] focus on one of our four questions: are speciation and divergence linked? They argue that there is strong evidence that divergence, particularly genetic divergence, often increases in punctuational bouts during the process of speciation. Importantly, they also suggest that this is true across the genome including the gene regions used to estimate phylogenies, which are usually thought to evolve neutrally [3,4]. We were far more circumspect about the causal relationship between speciation and divergence in our review (see [1], Box 2).

We completely agree with Venditti and Pagel that a correlation between speciation rates (or number of inferred speciation events) and genetic divergence, which has been found in a number of studies using phylogenetic data [3–5], is a very intriguing result and one that demands an explanation. Like them, we hope that our paper does not discourage other researchers from testing for this pattern in different groups and using different data.

We do hope, however, that our paper discourages researchers from interpreting such correlations between speciation rates and divergence as evidence that divergence accumulates via evolutionary pulses during the speciation process. We do not think there is sufficient evidence to draw such a conclusion. To support their suggestion that speciation is a ‘special time’ in evolution, Venditti and Pagel cite their earlier work to claim that ‘bursts of change associated with speciation may account for as much as 15–30% of the total evolutionary change’ [2,3]. However, this estimate is based entirely on the correlations between number of spe-

ciation events and genetic divergence. In order to make the jump from pattern to process, we need to look to other lines of evidence and in doing so, the argument for a link between the two becomes rather weak.

First, there is no compelling population genetic reason to suggest that the process of speciation should lead to increased rates of genetic change [6]. Although one might imagine that speciation occurring via the isolation of small populations should facilitate rapid genetic change, this argument was effectively dismantled in the debates surrounding ‘genetic revolutions’ a few decades ago [6]. A number of population genetic processes, such as change in effective population size or the strength/direction of selection, will cause rates of evolution to change [7] but there is no evidence to suggest that these processes are systematically different during the process of speciation compared to the background dynamics [5]. Venditti and Pagel cite changes in the rates of adaptation through time in experimental evolution [8] in support of their argument for the importance of speciation in molecular change; however, we think the opposite — in these cases, such changes occur within and across populations that are not undergoing speciation at all. Although some processes that trigger bouts of rapid genetic evolution (such as polyploidy) may be intimately associated with speciation, we see little reason to believe that a significant proportion of the correlation in rates between speciation and divergence at the phylogenetic scale is explained by such events.

Second, like in any correlation, the direction of causality is crucial to understanding the processes at work. When correlations exist, speciation may indeed be driving divergence, or speciation may simply be an occasional byproduct of divergence. Furthermore, correlations between net diversification and divergence could arise via decreased extinction rates rather than increased speciation rates. For example, reduced extinction probabilities may allow species to more easily traverse genetic and phenotypic landscapes and withstand higher mutation rates [9]. Similarly, species with higher mutation rates and evolvabilities may be more resistant to extinction [10].

Third, we should consider other factors that may lead to a correlation between genetic divergence and speciation

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rate; in our view, additional covariates are likely to be important in interpreting the correlations. Lineage-specific traits are known to influence rates of diversification [1] and molecular evolution [11] and it seems probable that the same traits may often influence both [12]. Overall, we think that even if the pattern is robust, the mechanisms which generate it remain poorly understood.

Like Venditti and Pagel, we think that this is an exciting time to be doing macroevolutionary research. Substantial progress can be made on many outstanding questions, including the causes of variation in rates of molecular evolution — but doing so will require formulating testable, clearly defined hypotheses based on sound population genetic reasoning.

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