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ON THE NATURE OF THINGS: ESSAYS

New Ideas and Directions in Botany

Past, future, and present of state-dependent models of diversification[1]

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Trait evolution and its effect on diversification have long been core questions in botany. de Saporta and Darwin, for example, discussed the evolution of insect pollination potentially leading to the "enigmatic" angiosperm radiation (Friedman, 2009). Many methods have been developed to address these questions, but Maddison (2006) strikingly demonstrated a potential issue with the way we think about the relationship between trait evolution and diversification rates (an issue raised by several earlier studies: Janson [1992]; Duda and Palumbi [1999]; Takebayashi and Morrell [2001]; Stireman [2005]). For instance, it is possible to mistake a bias in transitions (e.g., a greater rate of evolution from wind pollination to insect pollination than the reverse) for a difference in diversification rate (e.g., higher diversification rates for insect pollinated lineages). We could also make the reverse error of mistaking a bias in diversification rates between states as a difference in transition rates. Maddison et al. (2007) created a solution to this problem, the binary-state speciation and extinction model model, or "BiSSE" for short. This approach dealt with a single binary trait only; later work extended the model to deal with multiple state traits (MuSSE: FitzJohn, 2012a), continuous traits (QuaSSE: FitzJohn, 2010), geographic regions (GeoSSE: Goldberg et al., 2011), and to test whether change happens at speciation events or along branches (ClaSSE: Goldberg and Igic, 2012; BiSSE-ness: Magnuson-Ford and Otto, 2012). Collectively, they are referred to as state-dependent speciation and extinction (SSE) methods. We argue that while there is reason for concern in the use of these methods, they remain an important tool to consider.

A fundamental feature of all SSE models is that they are not models for only trait transitions, or for diversification only, but joint models for both. In other words, the data they seek to explain are the distribution of traits at the tips of the tree and the timing of speciation events that lead to extant species. This makes SSE models very different from those that seek to use, for example, sister group comparisons (Mitter et al., 1988) or other "shift" based tests (Sanderson and Donoghue, 1994) to look for the effect of potential "key innovations" on net diversification. These other approaches do not seek to model trait evolution, only the effect on diversification of those traits once they have evolved. Conversely, there are methods to estimate transition rates for traits (Pagel, 1994; Hansen, 1997; Ree and Smith, 2008), but they do not explicitly take into account the effect on diversification. They simply reflect a combination of processes, like mutation, drift, and selection within species that lead to transitions on a given tree.

Biologically, SSE models have a great deal of appeal in explaining trait patterns. When we observe that a particular character state has a high frequency, does this reflect a higher speciation rate or low extinction rate? Does it reflect a greater transition rate into rather than out of that trait, a slow rate of movement out of that trait in a group with that trait ancestrally, or just random chance with no influence of the focal trait at all? In theory, an SSE model can identify which of these factors play a role in a state's observed frequency (see Fig. 1). For example, Goldberg et al. (2010) found that in Solanaceae, species with self-incompatibility have a much higher diversification rate than those with self-compatibility. In fact, the diversification rate of self-compatible species was negative, meaning species are more likely to go extinct than speciate. Despite this, 57% of the species in their study were estimated to be self-compatible. Why would evolution result in a high frequency of a trait that tends to cause the extinction of groups possessing it? According to the model, the high frequency of self-compatibility comes about due to a high transition rate from self-incompatibility to self-compatibility through a breakdown of incompatibility mechanisms. Some combination of selection and drift within species leads to persistence of a trait that species-level selection would eventually eliminate. This sort of tension between processes happening within species and those happening between species can thus finally be directly addressed using SSE methods.

There are, however, an increasing number of concerns raised about the use of SSE approaches. Even in the initial paper describing them, it was clear that it would often be difficult to estimate extinction rates (Maddison et al., 2007). Recently, Davis et al. (2013) reported that for analyses with fewer than just a few hundred species, BiSSE has trouble detecting that diversification rates differ between traits, suggesting that much smaller but biologically

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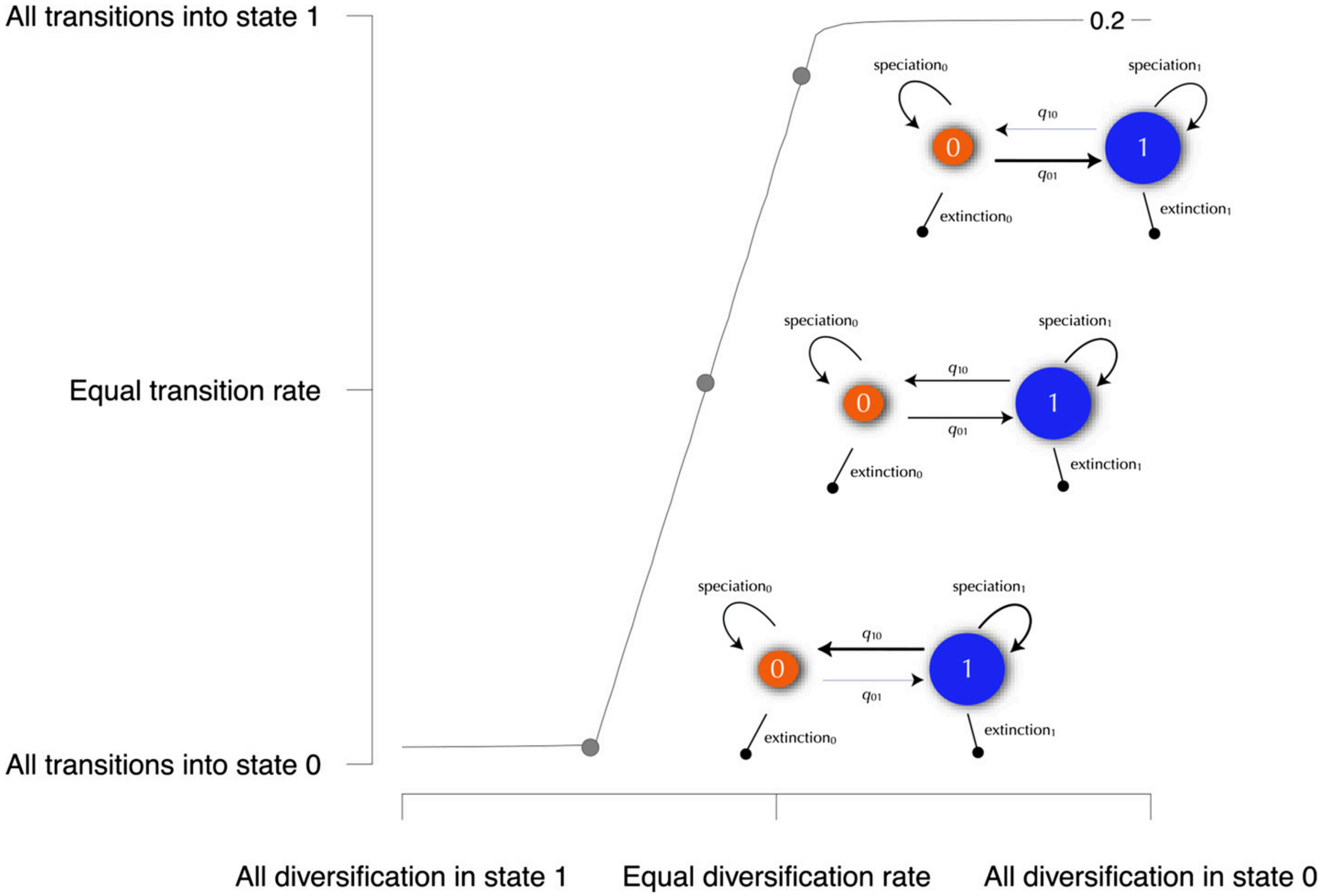

FIGURE 1 A contour line showing all combinations of rates that would result in an equilibrium frequency of 20% of the taxa having state 0 and 80% of the taxa having state 1 (as indicated by the area of the circles), in a state-dependent speciation and extinction (SSE) model. Three particular combinations of rates are highlighted to show how very different diversification and transition rates can lead to the same expected rarity of state 0. In the leftmost highlighted point, the transition rate going from state 1 to state 0 is an order of magnitude higher than the reverse rate, but the diversification rate in state 1 is nearly twice that of state 0—that is, state 0 is rare despite the high transition into this state. For the middle highlighted point, transition rates are equal, and the rarity of 0 is due to higher diversification rates in state 1. The rightmost highlighted point has a higher diversification rate in state 0 than state 1, but state 0 is still rare at equilibrium due to a very high transition rate from 0 to 1. A state can be rare at equilibrium despite having a higher transition rate into it, or despite a high diversification rate at equilibrium. Thus, SSE models can help tell what is actually leading to an observed disparity in state frequencies.

compelling clades, like, say, the Hawaiian silverswords, might not contain enough information to detect trait-based heterogeneity. There are also a wide variety of potential problems for diversification models in general (reviewed by FitzJohn [2012b]) that likely also apply to SSE models.

More severe criticisms of SSE approaches come from the interpretation of results. For example, if a question is framed as testing a null hypothesis, such as no effect of a trait on diversification, rejecting the null does not mean the alternate is true. This situation was shown dramatically by Rabosky and Goldberg (2015), who took empirical trees (thus, likely evolved under a complex, changing set of diversification parameters) and simulated a trait evolving on these trees with no relationship to diversification rates. In this situation, neither model available to BiSSE was correct: diversification rates do vary over the tree, but the simulated trait was not the cause of these differences. Models with the trait falsely linked to differential diversification were typically chosen and should raise a concern for biologists because even if a trait being examined in an actual study is unlinked to diversification, based on this work (and others, such as Maddison et al., 2007 and FitzJohn, 2012a), BiSSE methods will still likely indicate the trait has an effect on diversification.

While we have addressed this particular problem (Beaulieu and O'Meara, 2016), there will always be the risk that in cases where neither model is true, any inference is questionable. This is a general problem with models of any sort, but it has been most prominent in discussions of SSE because of their clear appeal in testing "key innovation" hypotheses. Examining whether the inferred model parameters produce data sets consistent with the empirical one is one way to investigate the adequacy of the model fit (Bollback, 2002; O'Meara, 2012; Pennell et al., 2015) but has yet to be fully adopted in the context of SSE analyses (but see Bromham et al. [2016]). The robustness of SSE inferences can also be assessed by using many models, rather than a simple null and a biologically informed alternative (Beaulieu and O'Meara, 2016). If multiple models with very different biological interpretations receive similar support, it may suggest that the mechanism described by the best model is nearly as credible as very different explanations, leading to appropriate caution.

Probably the most severe criticism of SSE methods, and similar methods based solely on transition rates (i.e., Pagel, 1994), is the problem of "phylogenetic pseudoreplication" pointed out by Maddison and FitzJohn (2015). In other words, if a trait has changed only once, or possibly just a few times, scientists could be misled about the effect of a trait on rates when it could be some other unmeasured trait(s) or merely chance. For example, consider a test of whether seed plants with carpels had a higher diversification rate than those without. SSE methods likely would infer higher diversification rates for angiosperms, which are the only lineages that have carpels. The problem is that even with the clear disparity in diversity between angiosperms and their likely sister clade, acrogymnosperms (the clade containing the four major extant lineages of non-angiosperm seed plants: conifers, gnetophytes, cycads, ginkgos), other factors changing along the branch leading to crown angiosperms could also explain this pattern. Higher diversification rates appearing somewhere within crown angiosperms, for instance, such as the origin of mesangiosperms (possibly as a result of further modifications to the carpel), could also create the illusion that angiosperms are more diverse due to some synapomorphy of the group (Smith et al., 2011). In either case, BiSSE would still map diversification rate differences based solely on the presence or absence of carpels. There is no single solution to all of these issues (though Rabosky and Huang [2016] attempted to solve the issue of the number of independent trait changes being ignored by these methods), but an important first step to remedy the situation is by examining traits that have changed multiple times with the clade. Even for those traits, however, one should check to see whether their effect on diversification is at least qualitatively similar every time they evolve (Beaulieu and Donoghue, 2013). For traits, like the carpel, that have evolved once, it now seems clear that SSE methods just cannot provide sufficient information to credibly accept or reject a hypothesis of their significance. Of course, there are many traits that have changed frequently across angiosperms, such as pollination syndrome, mating system, ploidy, etc. that are ideal for testing potential SSE-type patterns.

So, where does all this leave us in regards to the future utility of SSE models? It seems to us that the initial wave of interest and use of SSE models is quickly being replaced with widespread skepticism about their use. However, we feel the pendulum has unnecessarily swung too far in this direction. While SSE models have been subjected to very close scrutiny as of late, this scrutiny should only be recognized as an important step in establishing their very real limitations and potential ways to improve and extend them, not abandon them altogether. It is also important to remember that no model or method is without limitations, and for many questions, especially the evolution of diversification-affecting traits, SSE models should remain an important part of a botanists' toolbox for the foreseeable future. As we have stated elsewhere (Beaulieu and O'Meara, 2015), moving forward, we urge practitioners to use prudent caution, but do not abandon all hope.

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