

Magic traits: distinguishing the important from the trivial

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Servedio *et al.* [1], following Gavrillets [2], define a magic trait as ‘a trait subject to divergent selection and a trait contributing to non-random mating that are pleiotropic expressions of the same gene(s)’. This clarified definition is certainly helpful, but we outline here several pivotal questions for empirical research, particularly surrounding the crucial concept of effect size.

The effect size of a magic trait, defined by Servedio *et al.* [1] as ‘how much the trait contributed to the evolution of increased reproductive isolation’, determines whether a magic trait is actually important for speciation (an ‘important magic trait’) or is a ‘trivial magic trait’ (a magic trait of very small or zero effect size). Effect size is therefore what matters empirically, and yet it is absent from the definition of a magic trait, which instead embodies theoretical preoccupations with the genetics underlying traits. We do not propose to redefine ‘magic trait’, but instead hope to illustrate how empirical advances will require an explicit focus on effect size. Problematically, however, the definition of effect size is retrospective and not generally measurable; empirical proxies for effect size that can be used predictively are therefore needed. We here treat the strengths of divergent selection, assortative mating and pleiotropy (the three components of the magic trait definition) as the *a priori* expected contributors to effect size during speciation.

Divergent (including disruptive) selection, the first pillar of the magic trait definition, is certainly important for speciation; however, its magnitude is more important than its mere presence [3]. Moreover, distinguishing weakly divergent selection from the absence of selection is empirically difficult [4], making it hard to determine whether a trait is magic or non-magic. Fortunately, this distinction is probably not of key importance to the process of speciation, because magic traits under such weak selection are probably trivial. The empirical focus should be on magic traits expected to be of large effect size.

In addition, spatial and temporal variation in selection [5] makes it difficult to determine whether a trait is generally under divergent selection. For example, beak size in the Medium Ground Finch (*Geospiza fortis*) has been proposed to be magic [1,6], but selection on beak size is, at various times and places, directional, stabilizing, or divergent [7,8]. Consequently, it is hard to say whether beak size would satisfy the definition; as the selective regime changes, beak size switches from magic to non-magic and back again. This

implies that such a trait is, in a sense, an ordinary trait that contributes to non-random mating, but that is, at times, in a ‘magic environment’ that subjects it to divergent selection; the magic comes from the trait–environment interaction. Thus, a crucial question emerges: how consistently divergent, through time and across space, must selection be for a trait to be magic and also important for speciation? Again, we argue that expected effect size is the key: divergent selection must be sufficiently strong and consistent to actually drive divergence.

The second pillar of the definition is non-random mating. However, it is also difficult to distinguish weakly non-random mating from random mating (e.g. [9]), as well as to determine the specific trait underlying non-random mating [1]. Moreover, just as with divergent selection, non-random mating can vary in space and time [10]. Thus, all of the difficulties raised above concerning divergent selection apply with equal strength to non-random mating.

The arch connecting these two definitional pillars is pleiotropy; if, instead, the two pillars are influenced by a tightly linked pair of genes, that locus is considered only a magic trait ‘mimic’ [1]. Again, empirically differentiating between these two cases is quite difficult [11]. Furthermore, the distinction might be of little consequence to the dynamics of speciation; a mimic might have an effect size just as large as, or larger than, that of a magic trait [3]. Instead, what probably matters is the strength of pleiotropy or linkage.

In summary, empirically distinguishing trivial magic traits from non-magic traits, and magic traits from mimic traits, will prove very difficult. Fortunately, these distinctions are largely irrelevant to many questions surrounding speciation in nature. Instead, the important (although less precise) distinction is between traits expected to be of large effect size (whether magic or mimic) versus those expected to be of small effect size (whether trivial or non-magic). To bridge the gap between theoretical and empirical perspectives on magic traits, we suggest an increased focus on probable proxies for ultimate effect size, on the environmental and ecological factors that are likely to be contributing to effect size, and on the evolutionary forces expected to alter effect size through time. With these priorities, a better understanding of the magic of speciation can be expected.

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Magic traits, pleiotropy and effect sizes: a response to Haller *et al.*

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In our recent Review in *TREE* [1], we defined magic traits based on pleiotropy between divergent ecological adaptations and non-random mating. Haller *et al.* [2] imply doubt in the utility of this definition, concentrating their arguments on effect size (the contribution of a trait to the evolution of reproductive isolation, see [3]). They specifically make two points: (i) effect size is absent from the current definition of a magic trait; and (ii) magic traits of weak effect may be unimportant in speciation. We address each of these points in turn.

In general, definitions of biological phenomena are not conditioned on effect size, which would entail arbitrary cut-offs. For example, natural selection is defined as differences between individuals, based upon their traits, in viability or fecundity; this definition is not predicated upon such differences being large or even an important source of evolution in specific circumstances. Likewise, definitions of scientific concepts should not be affected by ease of measurement. Yet Haller *et al.* object that ‘distinguishing weakly divergent selection from the absence of selection is empirically difficult, making it hard to determine whether a trait is magic or non-magic’, and are concerned that it is empirically difficult to determine whether traits are pleiotropic. Natural selection itself is often hard to measure, but few would argue that ease of measurement should contribute to its definition (nor that the concept of natural selection is not useful as a result).

Can magic traits, defined by the presence of pleiotropy, be so weak as to be unimportant in speciation? We agree with Haller *et al.* that, under our definition, they can. For example, in our Review [1], we argue ‘it is very possible that some traits are “magic”; because they have the requisite pleiotropic effect but play a trivial role in speciation because of small effect sizes’. In the section ‘Effect size of magic traits’, we further elaborate upon the point that the importance of a magic trait in the speciation process depends upon both its contribution to a given component of pre-mating isolation and how much total reproductive isolation exists before the magic trait diverges; we conclude in our original Review that the importance of ‘magic traits with weak effects on late-evolving components of pre-mating isolation. . . might be trivial’.

Haller *et al.* object that such ‘trivial magic traits’ may be difficult to identify empirically, and that the distinction between them and non-magic traits is ‘largely irrelevant to many questions surrounding speciation in nature’. We caution that this conclusion is premature. Without knowing the actual distribution of effect sizes, it is too early to say which effect sizes are ‘important’ or ‘should be studied’. It may be the case that speciation often proceeds by the action of many genes of small effect sizes, so studying such genes will be important. Similarly, magic traits that are under weak divergent selection and/or play a small role in non-random mating might still have an important effect in speciation, perhaps because the timescale of speciation is long, or because they facilitate the divergence of other traits

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