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Review

Magic traits in speciation: 'magic' but not rare?

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Speciation with gene flow is greatly facilitated when traits
subject to divergent selection also contribute to non-
random mating. Such traits have been called 'magic
traits', which could be interpreted to imply that they are
rare, special, or unrealistic. Here, we question this as-
sumption by illustrating that magic traits can be produced
by a variety of mechanisms, including ones in which
reproductive isolation arises as an automatic by-product
of adaptive divergence. We also draw upon the theoretical
literature to explore whether magic traits have a unique
role in speciation or can be mimicked in their effects by
physically linked trait-complexes. We conclude that magic
traits are more frequent than previously perceived, but
further work is needed to clarify their importance.

Mechanisms of speciation

Speciation with gene flow continues to be controversial, in
part because it has been found to be theoretically difficult
[1–5]. The main argument is that gene flow and recombina-
tion randomize associations between genes under divergent
selection and those causing non-random mating (i.e. pre-
mating reproductive isolation). However, this selection–re-
combination antagonism disappears if non-random mating
is directly based on a trait under divergent selection. Such
traits have been referred to as 'magic traits' [4] to reflect that
a single trait is performing the functions normally attribut-
ed to two separate traits; in other words, the trait under
divergent selection and the trait causing non-random mat-
ing are one and the same. The adjective 'magic' can also be
interpreted to imply that such traits are unusual and, thus,
rare in nature. Nevertheless, magic traits are receiving
increased attention in both the empirical and theoretical
literature, although simultaneously there appears to be
some confusion about what exactly constitutes a magic trait.
It is therefore important and timely to review the existing
data and to clarify issues surrounding magic traits and their
role and importance in speciation.

What is a magic trait?

Even though magic traits are often studied purely at the
phenotypic level, a precise definition requires reference to

the underlying genetics. This is because magic traits are
encoded by 'magic genes', that is, genes subject to diver-
gent selection that also pleiotropically affect reproductive
isolation. The fundamental requirement of pleiotropy
guarantees an association between divergent selection
and non-random mating that cannot be broken by recom-
bination; this is what renders magic traits effective in
driving speciation with gene flow in theoretical models
(Box 1). Usually, one thinks of magic-trait genes as con-
trolling a single trait; many magic traits identified phe-
notypically will undoubtedly fall into this category.
However, this need not necessarily be the case. A complex
of two identifiable phenotypic traits, one under divergent
selection and one involved in non-random mating, can be
considered magic if the two component traits share a
common genetic basis. We collectively refer to both these
cases as a 'magic trait' (note that in the latter case, if the
traits are polygenic then pleiotropy can be partial, ren-
dering the trait complex partly magic).

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Box 1. Magic traits in mathematical models

''Pleiotropism. The gene pair.. adapting individuals to different niches may themselves cause assortative mating.. This seems very unlikely.'', p. 643 of [1].

As the above quotation by Maynard-Smith demonstrates, the concept behind magic traits has long been controversial. However, magic traits have commonly been assumed in theoretical models of speciation with gene flow [6,31]. In fact, the term 'magic trait' arose from controversy within the theoretical community about the realism of assuming that both reproductive isolation and disruptive selection are controlled by the same locus [4]. Many sympatric speciation models explicitly consider a single locus that controls both non-random mating and ecological fitness [1,39–42]. Others consider a single trait controlled by multiple loci that has dual effects on viability and reproductive isolation [43–45]. Similarly, models of reinforcement often include magic traits by assuming that the mating cue is under divergent selection [46–49], and many models of speciation based on habitat preference assume that individuals mate within the chosen habitat [15,50]. Typically, such assumptions are justified by arguing either that they are empirically plausible or that they are the 'best-case scenario' for speciation [39]. Nevertheless, there has been considerable debate over whether it is reasonable to concentrate on such models [3,4].

Although it is well recognized that magic traits will facilitate speciation with gene flow, few models compare speciation with magic and non-magic traits explicitly. An example of such a comparison is that of Dieckmann and Doebeli [43], who compared a magic-trait model of sympatric speciation with a model in which assortative mating was based on a marker trait initially unassociated with an ecologically relevant trait. They found that sympatric speciation occurred significantly more often when it was based upon a magic trait. Additionally, van Doorn and Weissing [35] explored the regime between magic and non-magic traits by continuously varying the strength of the pleiotropic effects of an ecologically selected locus on mate choice (a 'partly magic trait'). This study showed that a critical level of pleiotropy (i.e. the element that renders a trait 'magic') is required to induce speciation.

Box 2. Magic traits versus one- and two-allele mechanisms of speciation

In some cases, divergence of a magic trait is sufficient to induce reproductive isolation ('automatic' magic traits, Figure 1a). In others, though, reproductive isolation requires evolution at additional loci ('classic' magic traits, Figure 1b). As pointed out by Felsenstein [5], this can occur via one- or two-allele mechanisms, depending on whether the same or different alleles spread in two nascent species. For an example of a one-allele mechanism, consider the spread of an allele that induces assortative mating by self-referent phenotype matching (or an allele for sexual imprinting) in two nascent species that have already diverged in phenotype. An example of a two-allele mechanism is the evolution of divergent mating preferences (e.g. species A females have an allele for preferring large males, while species B females prefer small males).

It is not always clear how the distinction between one- and two-allele mechanisms relates to the discussion of magic traits. We argue that is it is useful to keep the two classifications (one- and two-allele mechanisms versus magic and non-magic traits) conceptually separate, because one refers to the genetic basis of reproductive isolation, whereas the other distinguishes between whether or not genes involved in reproductive isolation are subject to divergent selection [2,31,51]. Whether speciation proceeds via a one- or two-allele mechanism is, therefore, generally independent of whether any of the involved traits is a classic magic trait (we note that, even though 'automatic' magic traits necessarily contribute to reproductive isolation by a two-allele mechanism, they may act in concert with one-allele mechanisms that are responsible for a large fraction of total reproductive isolation).

Clearly however, some combinations of mechanisms may be more relevant than others in empirical systems. For example, if females prefer males with similar body size and body size is subject to divergent selection – a combination of a one-allele mechanism (self-referent phenotype matching) and a magic trait (body size) – then speciation will require only the divergence of body size and the evolution of strong size-assortative mating. In some cases, the latter may even pre-exist, as for example in species that have already evolved sexual imprinting. In contrast, speciation will be more difficult when a magic trait co-occurs with a two-allele mechanism; divergence of the magic trait will contribute to reproductive isolation only if other reproductive isolation loci (e.g. a preference locus) diverge as well. In this case, divergence will be more strongly opposed by gene flow.

Our definition of a magic trait requires that selection be divergent. By this we mean that selection favors different optima – either in different populations connected by some level of gene flow or within a single well-mixed population – and that selection supports the coexistence of the incipient species that are evolving towards these different optima. Usually, the source of such selection is assumed to be ecological (e.g. [6] use the term 'mating-ecology pleiotropy' synonymously with magic traits). However, in principle, the source of divergent selection on a magic trait could also be sexual selection, although it might be less conducive to supporting coexistence [7]. Our definition excludes from magic traits the related phenomena of traits leading to natal philopatry, reduced dispersal, or increased female choosiness, which can increase non-random mating but generally evolve via uni-directional, rather than divergent, selection. Furthermore, we note that the issue of whether or not a trait is a magic trait is independent from whether speciation proceeds via a one-allele or two-allele mechanism [5]. Both of these distinctions are important in determining whether or not speciation with gene flow is likely to occur (Box 2).

Finally, our definition of magic traits does not depend on how strongly they affect divergent selection, non-random mating or both, nor on how much they contribute to the evolution of reproductive isolation. However, in order to determine the significance of a magic trait to a speciation event it is critical to consider its 'effect size', that is, how much the trait contributed to the evolution of increased reproductive isolation, see [8] and below. Thus, as discussed below, it is very possible that some traits are 'magic' because they have the requisite pleiotropic effects but play a trivial role in speciation because of small effect sizes.

The diversity of magic traits

Both divergent adaptation and non-random mating can involve different kinds of traits and be driven by a variety of mechanisms, leading to a corresponding diversity of magic traits. In some cases, the evolution of traits under divergent selection leads to non-random mating as an unavoidable byproduct, whereas in other cases, the connection is less straightforward, as originally indicated by the term 'magic'. In the following, we will refer to these cases as 'automatic' versus 'classic' magic traits, respectively (see also classifications of pleiotropy in [9]).

Automatic magic traits

There are several scenarios where we can think of non-random mating as being 'built into' traits under divergent selection (Figure 1a). Although not usually thought of in this way, such traits qualify as magic traits, because one set of underlying genes controls both divergent adaptation
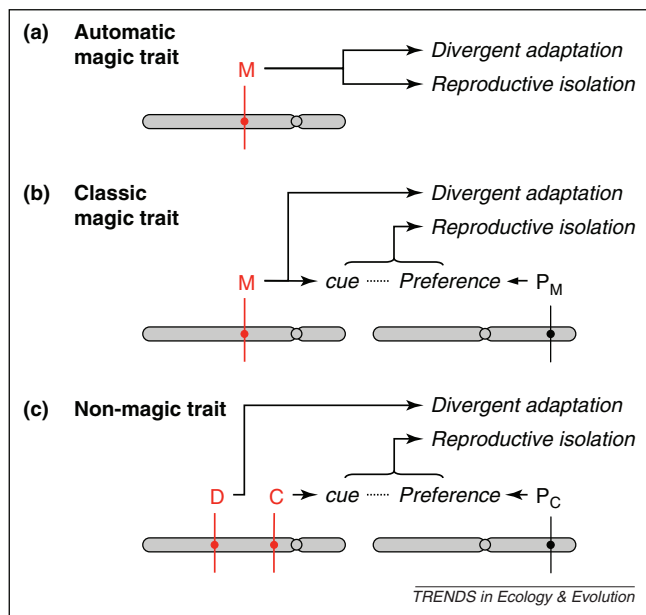
Figure 1. Schematic diagram of magic and non-magic traits. In (a), locus M codes for an 'automatic' magic trait. Divergence at this locus allows populations to adapt to different optima, and via a mechanism such as host choice or phenology, this process generates reproductive isolation as a byproduct. Panel (b) illustrates a 'classic' magic trait. Magic trait locus M affects a mating cue that is targeted by alleles at a preference locus, P_M, located elsewhere in the genome. Divergence at locus M is necessary but not sufficient to initiate speciation, as the evolution of reproductive isolation is (in this example) conditional on the evolution of specific alleles at the preference locus. In another scenario, it could be the preference that is under divergent selection and, therefore, constitutes the magic trait (see main text). In (c), speciation relies on divergence at the independent loci D, under divergent selection, and C, coding for a cue used for non-random mating, which can be on different chromosomes. As with magic traits, C can itself cause reproductive isolation, or it can require a separate mating preference, represented in the figure by P_C, a preference that targets the mating cue C. In principle, the loci C and D can mimic a magic trait if they are in complete or nearly complete linkage disequilibrium with each other (see discussion in main text). In all of these cases (a–c), the traits affecting divergent adaptation or reproductive isolation can also be polygenic instead of controlled by a single locus.

and non-random mating. For example, divergent selection on phenological traits automatically leads to assortative mating via temporal isolation, as can occur for flowering time differences in plants [10] and diapause emergence differences in insects [11,12]. Likewise, flower color might be an automatic magic trait if it is under divergent selection from sources other than pollination but different colors happen to attract distinct sets of pollinators (e.g. bees versus hummingbirds) [13]. Furthermore, selection on habitat choice can generate premating isolation when mating takes place in the habitat, as happens in many phytophagous insects [14]. This is the route by which sympatric speciation is thought to be most likely and has been demonstrated both theoretically [4,15] and in a laboratory experiment [16].

Under our definition, a very general class of magic traits arises whenever the ability of individuals to survive in a specific location generates assortative mating due to 'immigrant inviability' [17]. In such cases, traits conferring local adaptation are magic traits. An extreme example is provided by some ascomycete fungi [18]. These fungi can only infect specific host plants, and mating takes place on the host. Thus, if a strain evolves the ability to infect a new host, mating will automatically be assortative with respect to host use. Note that traits involved in local adaptation

can be different from those determining habitat choice, and that both types of traits can be magic. For example, in phytophagous insects, host adaptation ('performance') and host choice ('preference') might involve different traits, say morphology versus behavior, which are each independently subject to divergent selection and directly lead to assortative mating [19,20].

As suggested by the examples given above, automatic magic traits are likely to be common and might be important contributors to speciation. We do not provide an exhaustive review here, but stress that demonstrating such traits requires evidence that the trait under consideration is itself directly under divergent selection, as opposed to merely correlated with other traits under selection, see [21]. We also acknowledge that many of the above traits are not usually thought of as magic traits and that, precisely because they are relatively easy to envision, they are perhaps less intriguing than classic magic traits.

Classic magic traits
In contrast to the examples above, magic traits are perhaps most typically thought of as being caused by divergent selection acting on mating cues (such as color or body size; Figure 1b). Intuitively, this connection strikes many as unlikely, leading to the term 'magic trait' ringing true. Nevertheless, when searching the literature, we found 18 strongly suggestive cases where mating cues thought to affect sexual isolation were putatively involved in divergent adaptation (Table 1).

Finding conclusive evidence for a magic trait is difficult, because two different traits can be mistaken for a single magic trait if they are strongly correlated. Thus, two criteria must be met for a trait to qualify as a magic trait. First, the magic trait, not a correlated trait (controlled by different genes), must be subject to divergent selection. Second, the magic trait, not a correlated trait, must generate non-random mating. Therefore, in Table 1, we also review the strength of evidence supporting each putative example of a mating cue acting as a magic trait, with the strongest evidence requiring experimental manipulation. We find that the level of support varies widely and that the evidence tends to be weaker for the first criterion than for the second. In only one case have both criteria been met by manipulative experiments. For mimetic wing color-patterns in tropical *Heliconius* butterflies, Jiggins *et al*. [22] showed that individuals prefer to mate with live individuals and paper models of the same color pattern (Figure 2). Thus, divergence in color-pattern generates sexual isolation. Furthermore, both mark–recapture experiments [23] and manipulative experiments with paper models (R. Merrill, personal communication) indicate that coloration itself is subject to divergent selection, with different color patterns favored in different mimicry rings. In summary, both halves of the required evidence are present in this case, whereas in most other potential examples of magic traits, more work is needed to provide unequivocal evidence.

Just as divergent selection can act on mating cues, magic traits can also arise when divergent ecological selection acts on mating preferences, rather than cues (Figure 1b). If different local environments exert different selection pressures on the sensory system (e.g. perception

Table 1. Examples of putative 'magic traits', restricted to those involving mating cues[a].

System	Divergent forms	Putative magic trait(s)	Putative cause of divergent selection	Criterion 1: ecological selection	Criterion 2: mate choice	Refs.
1. *Gasterosteus* Freshwater sticklebacks	Limnetic and benthic forms	Body size	Foraging niche, competition	Experiment	Manipulative Experiment	[65,66], Conte and Schluter, personal communication
2. *Gasterosteus* Stickleback fishes	Freshwater and marine forms	Body size	Foraging niche, competition	Observational	Manipulative experiment	[67,68]
3. *Gambusia* Fishes	Predator and predator-free forms	Body shape	Predation regime: predators present versus absent	Observational	Experiment	[69]
4. *Littorina* Intertidal snails	Upper and lower shore ecotypes	Body size	Crab predation	Experiment	Experiment	[70,71]
5. *Heliconius* Mimetic butterflies	Different mimetic forms	Color-pattern	Visual predation (mimicry)	Manipulative experiment	Manipulative experiment	[9,22,23], Merrill personal communication
6. *Dendrobates pumilio* Poison-dart frogs	Different mimetic forms	Color and color-pattern	Visual predation (mimicry)	Observational	Manipulative experiment	[72–74]
7. *Mimulus* Monkeyflowers	Bumblebee-pollinated *Mimulus lewisii* and hummingbird-pollinated *Mimulus cardinalis*	Flower color	Divergent habitat types and pollinators	Observational	Manipulative experiment	[13,75]
8. *Geospiza* Darwin's finches	Ecologically-divergent species pairs	Beak morphology, which affects song, and body size	Foraging niche, competition	Experiment	Manipulative experiment	[76–80]
9. *Hypolectrus* Marine Hamlet fishes	Variable color-morphs	Color-pattern	Aggressive mimicry	Observational	Observational	[81]
10. *Lycaeides* Butterflies	Wet meadow adapted *Lycaeides idas* and dry habitat adapted *Lycaeides melissa*	Wing color-pattern	Unclear	Observational	Manipulative experiment	[82]
11. *Gasterosteus* Sticklebacks	Unimodal solitary populations	Diet	Foraging niche, competition	Observational	Observational	[83]
12. *Loxia curvirostra* Crossbill birds	Different 'call types'	Foraging rate, performance	Foraging niche	Experiment	Manipulative experiment	[84,85]
13. *Carpodacus mexicanus* House finch	Native Sonoran desert and urban areas	Bill morphology	Foraging niche	Experiment	Observational	[86]
14. *Hippocampus subelongatus* Western Australian seahorse	A population	Body size	Mating system linked to male pregnancy	Observational	Observational	[87]
15. Mormyridae African weakly electric fish	Different electric discharges	Electric organs discharge	Electrolocation, electrocommunication	Observational	Manipulative experiment	[88]
16. *Satsuma* Snails	Chiral forms	Direction of shell coiling ('chirality')	Snake predation	Experiment	Experiment	[89,90]
17. *Hyalella azteca* Amphipods	Size ecotypes	Body size	Presence or absence of fish predation	Observational	Observational	[91]
18. *Rhinolophus philippinensis* Horseshoe bats	Different sympatric size morphs	Echolocation	Ability to attack different types of prey during foraging	Observational	Observational	[92]

[a]Each example was evaluated according to the two criteria required to demonstrate a magic trait, and categorized as to how strongly each criterion was met. For selection, these categories in order of increasing strength of evidence were: (1) observational evidence stemming from trait divergence between habitats, often bolstered by functional considerations, (2) experimental evidence stemming from measurements of selection on the trait, but where manipulations were not applied to rule out selection on correlated traits, and (3) manipulative experiments were used to control for correlated traits, demonstrating the trait itself was subject to selection. For mate choice, these categories were: (1) observational evidence stemming from assortative mating based on the trait in nature or indirect inferences about preferred trait values during mate choice, (2) experimental evidence stemming from mate choice experiments in the lab, but where manipulations were not applied to rule out mate choice on correlated traits, and (3) manipulative experiments were used to control for correlated traits, demonstrating the trait itself affected mate choice.
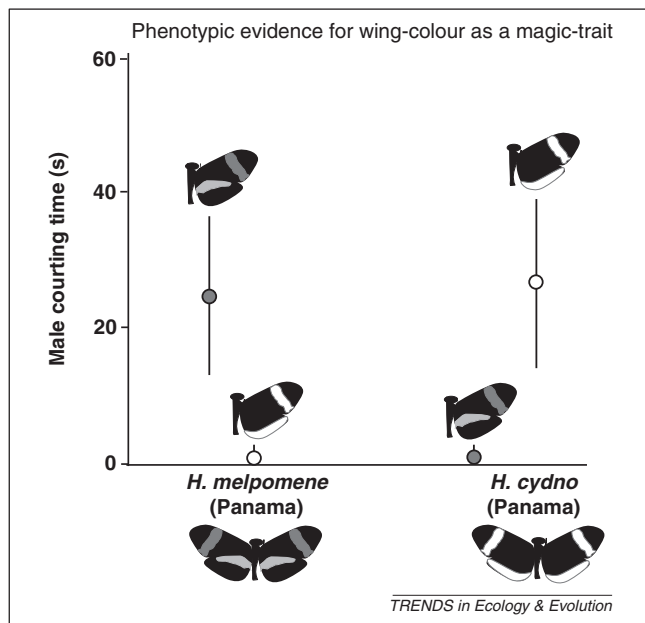
Figure 2. An example of a magic trait. Mimetic color-patterns in *Heliconius* butterflies are under divergent selection to adapt to different models and these color patterns also affect mate choice such that individuals prefer to mate with individuals of the same color-pattern. Shown here is the mean (± 95% confidence intervals) time spent courting live females in 10-minute trials. Similar results were observed using paper color-pattern models. Adapted with permission from Macmillan Publishers Ltd: Nature [22].

of different wavelengths of light in different parts of a forest canopy), then these can in turn affect the way individuals perceive potential mates. Viewed in this way, putative examples of speciation by 'sensory drive' might involve magic traits. We do not include these examples in Table 1 (instead restricting it to mating cues), because sensory drive has been reviewed extensively elsewhere and found to be relatively common [24,25]. Note, however, that even if preference is a magic trait, speciation still requires divergence in the corresponding mating cues. We also stress that, just as with cues that act as magic traits, 'magic preferences' must be convincingly proven to be both under divergent selection and involved in reproductive isolation.

A broad class of traits with a close relation to magic traits are mating cues with condition-dependent expression. This is because condition-dependent expression is likely to be affected by ecological divergent selection. For example, if locally adapted males are in good condition and can reliably increase their attractiveness by expressing a condition-dependent (costly) ornament, females will be able to select locally adapted mates once they evolve a corresponding mating preferences [7]. A putative example of this mechanism exists in *Drosophila*, where males have higher mating success when they are adapted to their current thermal environment [26]. In the above scenario, the trait responsible for local adaptation acts identical to a magic trait, because it affects reproductive isolation by modifying the expression of the condition-dependent mating cue. In contrast to a true magic trait, however, the association between mate choice and ecological adaptation relies on genotype–environment interaction and can break down in the face of migration.

Genetic studies of magic traits

The evidence for magic traits discussed above stems from phenotypic data. However, because magic traits are underlain by pleiotropic genes, additional insight could be gained from genetic studies. For example, to isolate magic-trait genes, repeated backcrossing can be used to generate 'near-isogenic lines' (NILs), which differ primarily (or only) in a gene of interest. These NILs can then be used for experimental demonstration that this gene has the pleiotropic effects characteristic of a magic trait (gene). Bradshaw and Schemske [13] applied this procedure to two species of monkeyflower with different flower colors. Flower color is controlled in large part by a single QTL locus (*YUP*); consequently, NILs that differ genetically in only the small proportion of the genome (3%) containing this locus have flowers with different colors. Furthermore, substitution of the *YUP* allele from the hummingbird-pollinated *Mimulus cardinalis* into the bumblebee-pollinated *Mimulus lewisii* increased the attractiveness of *M. lewisii* to hummingbirds and pleiotropically decreased its attractiveness to bumblebees, thereby facilitating the evolution of pollinator isolation. Likewise, introgression of the *M. lewisii YUP* allele into *M. cardinalis* increased the attractiveness of *M. cardinalis* to bumblebees. While this suggests that YUP is a magic-trait gene, conclusive evidence would still require demonstration that flower color itself is under divergent selection (from a source independent of pollinator preference), as well as ruling out a role for tightly linked genes in the introgressed region. Finally, even if *YUP* is a magic-trait gene, the question of its importance for speciation (i.e. effect size) remains.

Magic traits might also be inferred from candidate genes, which can be identified based on functional considerations or geographic variation in allele frequencies. A putative example is provided by Seehausen *et al.*'s [27] study of opsin genes in two Lake Victoria cichlids, *Pundamilia pundamilia* and *Pundamilia nyererei*. Opsins are a common component in color perception, and the lake is spatially highly heterogeneous in water clarity and ambient light. Seehausen *et al.* [27] document that fish populations living in different light regimes possess divergent ecological adaptation in their visual system, based on genetic divergence in the long-wave sensitive opsin gene (*LWS*). Populations in different environments were also shown to often exhibit moderate to strong reproductive isolation, which is at least partly due color-assortative mating. However, the evidence that assortative mating is directly affected by the *LWS* genotype is statistically non-significant. Although further work is required to determine the extent to which *LWS* is a true magic-trait gene, this example demonstrates the utility of genetic data for studying magic traits.

The importance of magic traits

We have presented evidence that both automatic and classic magic traits might be more widespread than previously appreciated. However it is not clear what overall contribution such traits make to speciation. The answer to this question will depend on the effect size of magic traits, whether they can be mimicked by complexes of non-magic traits, and how they interact with non-magic traits.

Effect size of magic traits

Even when they are present, the importance of magic traits in speciation depends on the degree to which they cause an increase in reproductive isolation, i.e. their 'effect size', see [8]. Magic traits that are statistically-identifiable in observational and experimental studies (e.g. those in Table 1) most likely constitute a relatively large source of premating isolation between populations. Reproductive isolation can, however, consist of multiple components, not all affected by the magic trait [10,17,28]. Moreover, some components of reproductive isolation might evolve after the evolution of barriers to gene flow is complete. Thus, the effect of a magic trait on speciation must be assessed in the context of (1) how strongly the trait affects a component of premating isolation, and (2) how much total reproductive isolation already exists when a magic trait diverges between populations. Magic traits with strong effects on early-evolving components of premating isolation could result in a large increase in total reproductive isolation, and thus be of critical importance for speciation. In contrast, magic traits with weak effects on late-evolving components of premating isolation will cause little increase in reproductive isolation (i.e. will have small effect sizes), and their importance might be trivial.

Can magic traits be mimicked by complexes of non-magic traits?

Critical to the importance of magic traits is the question of how unique their role is in speciation. Theoretical models predict that speciation without magic traits (Figure 1c) can be difficult due to recombination, which destroys associations between the loci responsible for divergent adaptation and those affecting reproductive isolation [4,5]. However, the force of recombination is reduced if the loci involved are physically linked, suggesting that there might be a continuum in the degree to which complexes of non-magic traits can mimic the role of magic traits in the speciation process. Here, the underlying idea is that strong linkage disequilibrium between a pair of loci – one subject to disruptive selection and the other affecting reproductive isolation – can substitute for the pleiotropy characteristic of true magic traits, because it causes divergent selection on one trait to 'spill over' to the trait affecting non-random mating, thereby driving the evolution of reproductive isolation [2,4,29,30].

Under weak selection, linkage disequilibrium decays on a timescale that is inversely proportional to the rate of recombination, implying that high levels of linkage disequilibrium can be maintained for significant amounts of time between loci located in genomic regions of reduced recombination (Box 3). However, this argument leaves two

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Box 3. Non-magic traits and low recombination

As described in the main text, complexes of non-magic traits might mimic magic traits if the underlying genes (i.e. genes undergoing divergent selection and other genes generating non-random mating) are tightly physically linked. Such tight linkage is most likely if the genes involved are sex-linked or reside in a genomic region of low recombination, e.g. close to centromeres or within a chromosomal inversion [52]. For the case of inversions, introgression is reduced for large regions of the genome because recombination in heterozygotes produces abnormal chromatids, which typically cause developmental problems in the offspring. Therefore, inversions might protect linkage disequilibrium from being broken up, at least for some period of time [53], even if the underlying genes are not located very close to each other [52,54,55].

Genetic studies have examined the effectiveness of regions of low recombination in facilitating the maintenance of high levels of linkage disequilibrium. A number of studies have now reported that genes involved in divergent adaptation and reproductive isolation (or strongly differentiated anonymous loci) reside in chromosomal inversions [54,56–59]. However, even single study systems provide evidence both for and against the view that regions of low recombination promote genetic divergence (Table I). Additionally, recent population genomic studies show that genes putatively affecting adaptive divergence or reproductive isolation are often widely-distributed across the genome, rather than clustered within one or a few regions of presumably low recombination, for review see [60]. In summary, evidence is currently mixed with regard to whether low recombination often renders the action of non-magic traits similar to that of magic traits, inviting further study.

Table I. Examples of single study systems where (a) some lines of evidence support a role for factors which reduce recombination in promoting genetic divergence and the maintenance of strong linkage disequilibrium, but (b) some data indicate factors which reduce recombination are not critical for genetic divergence.

Study system	(a) Finding supporting a role for reduced recombination	(b) Finding arguing for a more limited role for reduced recombination	Refs.
1. *Helianthus annuus* and *Helianthus petiolaris* sunflowers	Genetic divergence is accentuated near chromosomal breakpoints, where recombination is predicted to be most extensively reduced.	Average genetic divergence across inverted versus collinear regions did not differ and widespread adaptive differentiation of collinear regions was observed.	[61]
2. *Rhagoletis pomonella* apple and hawthorn host races	Genetic divergence is accentuated within inverted regions, relative to collinear ones.	The magnitude of elevated genetic divergence in inverted regions was moderate. Provides direct experimental evidence for widespread adaptive divergence across most collinear regions.	[37]
3. *Anopholes gambiae* molecular forms	Only three strongly differentiated genomic regions were detected, the largest of which lies in proximity to a centromere.	Two strongly differentiated regions are not within regions of known low recombination.	[62]
4. *Drosophila pseudoobscura* and *Drosophila persimilis* fruitflies	Genetic divergence is somewhat accentuated within inverted regions, relative to collinear ones.	Marked accentuated genetic divergence in inverted regions, relative to collinear regions, is apparent only near chromosomal breakpoints, suggesting the 'window of influence' of inversions is small.	[63,64]

issues unresolved. First, to assess the empirical relevance of non-magic trait complexes relative to magic traits, it is necessary to estimate the likelihood that the loci underlying a non-magic trait complex co-localize in a region of sufficiently low recombination. How probable this is depends on the timescale required for speciation, the number of genes affecting either reproductive isolation or divergent adaption, their genomic distribution, and the genetic mechanisms that might exist to create non-magic trait complexes *de novo* (e.g. gene translocation or the capture of genes by chromosomal inversions). Second, this argument assumes that linkage disequilibrium in a non-magic trait complex is strong from the outset of its involvement in speciation. This is only likely to be the case upon the secondary contact of populations that have diverged in allopatry [4,31]. In other biogeographic contexts, tight physical linkage would actually oppose speciation, at least initially, by delaying the build-up of linkage disequilibrium.

Given that none of these factors is currently known in much quantitative detail, it seems premature to argue either strongly for or against a unique role for magic traits in speciation. However, there is currently some data on genomic co-localization: QTL mapping studies have reported that traits under divergent selection and traits affecting premating isolation map to the same chromosomal location (e.g. in *Heliconius* [32] and *Acyrthosiphon pisum* pea aphids [33]) Further work might determine whether these represent cases of physical linkage or pleiotropy (i.e. true magic traits). In general, it might be that only some QTL will map to the same genomic region while others do not, indicating that even in the case of pleiotropy, the trait complex might be only partly magic.

Interactions between magic and non-magic traits
Regardless of whether or not non-magic traits can mimic magic traits, both types of traits can play important roles in establishing larger assemblages of genes that drive speciation. During the early stages of speciation, true magic traits, if present, might be expected to diverge relatively easily. In turn, the underlying divergently-selected loci might be surrounded by a genomic region (i.e. window) of reduced gene flow, in which the effective recombination rate between populations is potentially diminished via the process of 'divergence hitchhiking' [34]. Thus, as the genes underlying magic traits diverge between populations, the effective rate of recombination and gene flow between the incipient species will be reduced, potentially creating or reinforcing associations between magic and non-magic traits, and among different sets of non-magic traits [35,36]. This mechanism can lead to a gradual build-up of reproductive isolation and adaptive diversification, creating ever more favorable conditions for loci with loose linkage to contribute to speciation. As the process proceeds it eventually leads to genome-wide linkage disequilibrium [36]. As divergence hitchhiking is most effective when the number of loci under divergent selection is at least moderate [36], these arguments suggest a potential role for magic traits with a polygenic basis. They also show that, even if a particular magic trait initially has a small effect size, it might ultimately be important in speciation if it can facilitate

divergence at other loci. Empirical studies testing these predictions will need to determine, preferably via experiment, how many loci are subject to divergent selection and differentiate during the speciation process, see [37].

Conclusions
Speciation can be facilitated when ecological and mating traits act in concert. Although magic traits are often thought of as a somewhat artificial construct of theoretical models, we have reviewed several mechanisms by which traits under divergent selection are, indeed, able to generate reproductive isolation, either as an unavoidable by-product of divergence or in less automatic ways. Even in the perhaps more captivating category of 'classic' magic traits, preliminary evidence is accumulating for a number of examples. Nevertheless, it is important to realize that there are also numerous counter-examples to magic traits: traits under divergent selection that do not affect mate choice [38]. It would be of great interest to determine what proportion of divergently-selected traits are magic: the greater, the more likely that speciation with gene flow will be common. However, this data is currently not available.

We also discussed the relative contributions that magic and non-magic traits might have in the speciation process. We argued that, in the extreme situation of tight physical linkage coupled with strong, previously established linkage disequilibrium, complexes of non-magic traits have the potential to mimic magic traits in their effects. Nonetheless, so long as associations between the component traits depend on linkage disequilibrium rather than pleiotropy, they can erode with time. It remains unclear how strongly such complexes of genetically associated non-magic traits facilitate speciation during the period in which they exist. Finally, further data are required on how magic traits contribute to different points in the speciation process, and how they might affect the rate and stability of speciation.

In conclusion: how magic are magic traits? Because more studies are necessary to determine whether magic traits can be effectively mimicked by complexes of non-magic traits, it is too early to tell whether magic traits are truly 'magic' in having a unique role in speciation. Evidence is accumulating, however, that they are not magic in the sense of being rare in nature.

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