

are obtaining extra-pair young' and he suggests that these data disagree with predictions from the good genes hypothesis. However, under the good genes hypothesis, we expect females to base their choice for extra-pair copulations on their assessment of the relative quality of their own mate versus the available extra-pair males (i.e. usually their neighbours). Thus, quality should not be seen in an absolute sense, but relative to other options available for each female. Ideally, pairwise comparisons of the characteristics (quality) of within-pair and extra-pair males from the same nests should be made, such as those in the recent study of great reed warblers (*Acrocephalus arundinaceus*)¹.

We suggested, under the genetic quality hypothesis, that low levels of extra-pair paternity might be expected in populations that had undergone a bottleneck, because genetic quality differences among males would be low. Cordero suggests there are alternative explanations. According to the 'heterozygosity' theory, females choose mates to avoid the expression of lethal or deleterious genes by producing heterozygous rather than homozygous offspring. This theory does make predictions about the frequency of extra-pair copulations in relation to the overall genetic diversity in populations, but in the opposite direction to that expected from genetic quality benefits. In populations with lower genetic diversity, the risks of inbreeding depression are higher and, therefore, females might be more likely to seek extra-pair matings if the main benefit is the production of heterozygous offspring.

We agree that avoiding inbreeding effects or genetic incompatibility is important for a female and might explain some multiple mating patterns (such as when a female has several extra-pair partners). However, it is not yet clear whether these mechanisms, by themselves, can maintain the high variance in male mating success, which is a feature of species with high levels of extra-pair paternity². It is this nonrandom distribution of matings that provides the evolutionary force necessary to produce the sexual ornaments characteristic of populations with extra-pair paternity³ and that is more readily explained by genetic quality benefits.

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Key innovations?

Hunter's *TREE* review⁴ of 'key innovations' raises several concerns:

(1) Most definitions of key innovations portray them as playing a causal role in diversification. They are identified as adaptive features present in all members of a diverse clade and, by implication, in the clade's ancestor. But how is a clade delineated? A clade is diagnosed by synapomorphies implicitly present in a common ancestor. So, the features used to define a clade are also advanced as the explanation for its existence – thereby confusing correlation and causation.

(2) Hunter's terminology ignores the 1980s revolution in macroevolutionary theory – particularly his reference to 'successful' clades seizing 'opportunities' to diversify into new 'adaptive zones'. Hierarchy theorists laboured to expunge such ideological thinking. Vrba's 'effect' hypothesis² argues that apparently 'successful' clades are actually intolerant clades; their members have narrowly defined resource requirements, and environmental change exposes them to negative selection (mortality or reproductive failure). Can such a clade sensibly be labelled more successful than a more tolerant group (which can roll with the punches), which is consequently species-poor and likely to persist in the face of habitat deterioration?

(3) This value-laden terminology points to a confused model of speciation and/or radiation. The most enduring conflict of evolution concerns the role of natural selection in the origin of species. Key innovations imply features that enhance survival or reproduction in the face of competition, predation or environmental challenge. If key innovations are a cause of radiation, it must be in one of these contexts. However, there is little evidence to support such a claim³. Adherents of both the traditional synthesis^{4–6} and the expanded macroevolutionary synthesis^{7,8} argue that radiation is more rapid and more extensive in the absence of competitor and predator pressure, for example on oceanic islands or in the period immediately following a mass extinction. Furthermore, Hunter's review indicates that the role of key innovations is to allow organisms to escape these very sources of selection, leaving environmental challenge as the sole directional pressure driving diversification.

If key innovations allow taxa to invade new adaptive zones, they must arise before such invasions and without the benefit of direct selection by the environment to which they are fortuitously suited. They are true exaptations⁹. We have no difficulty believing the concept that an exaptation might allow a population to persist under altered environmental conditions; this is the essence of Darwin's model. What we fail to see is why an exaptation should 'promote speciation'. Why should the possession of a fortuitous character that has allowed a population to survive one punishing round of selection, provoked by exposure to a novel environment, now inspire its descendants to invade new and different environments with similarly destructive consequences? Isn't it more likely that the real factor promoting speciation is not the key innovation but the same kind of environmental change that destroyed the population's habitat in the first place, forcing it to adapt to a new niche?

The concept of key innovations does more to confuse macroevolution than to clarify it.

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Reply from J.P. Hunter

I agree with Masters and Rayner on three points. First, the search for key innovations might become circular if one merely assumes that synapomorphies of diverse clades are key innovations, which is why I warned against such assumptions (Ref. 1; Box 3). The test of a key innovation lies in its functional attributes and association with radiation in (preferably) multiple replicate lineages and not in its usefulness in reconstructing phylogeny. Some key innovations are indeed rather homoplastic (Ref. 1; Box 4). Second, species richness is not the sole measure of 'success'. Rather, success can be measured in many ways, including species longevity, phenotypic diversity, abundance and even biomass¹, all of which imply expansion in the use and control of energy². Third, I have argued^{1,3} that some key innovations are exaptations that allow a lineage 'to persist under altered environmental conditions'. Enhanced survivorship promotes diversification because extinct species can neither speciate⁴ nor 'invade new and different environments'. Exaptations need not promote speciation when they can operate equally well by lowering extinction rate.

Masters and Rayner oversimplify when they characterize the consensus opinion to be that competition inhibits diversification. Competition is indeed commonly modeled as inhibitory⁵, and exponential diversification is the null expectation in the absence of pre-emptive competition and other constraining factors⁶. However, competition may also escalate adaptation⁷ and drive character evolution during adaptive radiation^{8,9}, particularly in low density environments, such as on oceanic

islands¹⁰ and after mass extinctions^{6,11}.

Competition can have positive as well as negative effects on diversity, although positive effects are difficult to distinguish from other factors over large time scales.

Do key innovations allow escape from selection pressures? In the adaptive trade-off model¹¹, key innovations reduce the costs associated with adaptation to conflicting selection pressures (often by decoupling previously linked functions), thereby allowing natural selection to operate with greater efficacy. In the escalation model, key innovations allow a temporary (not permanent) escape from competition, predation or parasitism pressure until enemies evolve counteradaptations (Ref. 1; Box 4). In neither model is there a permanent escape from these sources of selection.

Research on key innovations is not so much concerned with what causes radiation but why some groups radiate and others do not. What does cause radiation? 'Causes' are the conditions that bring about a result, but conditions can be either necessary, sufficient or both to produce that result. 'Environmental challenge' cannot be sufficient to produce a radiation because, in the absence of ecological opportunity, any environmental challenge that destroys a species' habitat is likely to result in extinction not radiation. Ecological opportunity, which is necessary for radiation¹², seems to depend both on the available ecological space and the organisms' ability to use that space – often through key innovations.

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Hybrids and hybrid zones

Arnold's new book on hybridization¹, recently reviewed by Ritchie in *TREE*², has brought attention to an old, controversial but revitalized topic in evolutionary biology. The two reviews^{2,3} we have read share a sceptical attitude towards studies of hybridization lying outside the hybrid zone theory. They consider Arnold's book too 'opinionated'² and 'an argument for a greater emphasis on the positive role of hybridization in evolution' rather than a 'comprehensive review'³. However, one of the merits of the book is that it devotes a great deal of effort towards reconciling divergent approaches to the topic. Arnold dedicates equal importance to animal and plant studies, as acknowledged by Ritchie², and also puts much emphasis on the analysis of hybrid zones. In fact, when proposing a model for the birth of new evolutionary hybrid lineages he places his 'new conceptual framework (the evolutionary novelty model)' within the hybrid zone framework. Our criticism of this proposal is that it may be too rigid to fit scenarios departing from the specific model of hybrid speciation proposed by Grant⁴, that is, recombinational speciation.

In our opinion, relying exclusively on the hybrid zone framework to assess the role of hybrids in evolution is misleading. Hybrid zones usually imply relatively recent events and species with strong reproductive barriers. The tension zone model assumes that hybrid zones are maintained by a balance between selection against hybrid individuals and dispersal of parental individuals into the hybrid zone⁵. As we allow other factors (basically, interactions between the hybrids and a heterogeneous environment) to play a role in the model, we move into the other interpretation of hybrid zones. The latter, often called the bounded-hybrid-superiority model, seems more accurate – at least when applied to plants⁶. Yet, dedicating much effort to studying the genetic and ecological factors involved in the maintenance of hybrid zones does not justify neglecting the ample molecular and morphological evidence available.

From a pattern-oriented approach, it is true that reticulation may preclude a ready interpretation of results and that alternative explanations, such as 'lineage sorting following speciation in a polymorphic ancestor', are sometimes possible. Adopting a phylogenetic approach has risks and difficulties, some of which are inherent to the subject of hybridization: (1) phylogenetic inference methods are designed to detect hierarchical structure resulting from divergence; (2) no single predictable pattern can undeniably reveal the occurrence of reticulation. However, a combination of different sources of data may be conclusive to document reticulate evolution as the references gathered in Arnold's book convincingly show. Certainly, the difficulties involved in a phylogenetic approach do not justify Ritchie's untenable statement that 'most of the evidence of the significance of hybridization relies on well studied hybrid zones'² nor his conclusion that he 'need[s] more persuading that hybridization is a creative force in speciation before [he] can recommend this [book] as essential primer reading'.

We do not claim that the pattern-versus-process dichotomy is all that matters in the way the impact of hybridization is perceived. Process-oriented studies have produced insights both at the genomic and populational levels. Our point is that this kind

of study, as exemplified by the excellent research on sunflowers⁷ and Galápagos finches⁸, need not be immersed in the hybrid zone paradigm.

The hybrid zone approach is a critical avenue to study the initial stages of the formation of hybrid lineages under certain circumstances. However, relying exclusively on studies framed by the hybrid zone theory is insufficient for a comprehensive perception of a complex phenomenon like hybridization. Furthermore, it is certainly inadequate to test or document the occurrence of past events of reticulation between divergent lineages.

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Reply from M.G. Ritchie and N.H. Barton

Nieto and Fuertes seem to be under the impression that our reviews^{1,2} of Arnold³ sought to imply that hybridization is best studied solely in the context of hybrid zone theory. This was not the case. Indeed, a quotation from Ritchie they describe as 'untenable' comes from a paragraph more fully quoted as 'there must be many cases which do not fit a zonal model, when intermittent hybridization occurs, occasionally resulting in establishment of a hybrid genotype. ... the rarity of [such] hybridization events makes them difficult to detect, so most of the evidence of the significance of hybridization relies on well studied hybrid zones'. Clearly, the intention was not to state that hybridization had to be studied in the context of hybrid zones, but rather that it is usually easier to identify and study the outcome of hybridization where there is unambiguous evidence that this has occurred.

Nieto and Fuertes raise two important issues. First, they place 'pattern-oriented' approaches in opposition to 'process-oriented' studies: a 'phylogenetic approach' infers past hybridization, whilst the 'hybrid zone framework' addresses the processes that keep hybridizing taxa distinct. These approaches are complementary, both being necessary for a full understanding of short- and