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Hybridization, transgressive segregation, genetic covariation, and adaptive radiation

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Analysis of adaptive radiation has had a central role in the development of evolutionary theory, but it is not clear why some groups radiate and others do not. Two recent papers by Albertson and colleagues on the genetic architecture of East African cichlid fishes implicate hybridization, transgressive segregation and genetic covariation in the early stages of adaptive radiation. Transgressive segregation and genetic covariation might be key innovations in genetic architecture that favor adaptive radiation.

Hybridization between members of conspecific populations and closely related species is common and has important evolutionary consequences [1]. One possible consequence is transgressive segregation (Box 1), which produces hybrid phenotypes that exceed the phenotypic range of the parental species and which might be a common phenomenon [2]. Transgressive hybrids can be sufficiently divergent from both parental species to establish a new hybrid species that can coexist with both parental forms. The potential for hybrids to found new species is enhanced if functionally related traits do not segregate independently, conserving associations (i.e. morphological integration; see [3]) among those traits in hybrid progeny. Seehausen [1] proposed that, when sympatric or parapatric species are genetically similar and readily hybridize, transgressive segregation can be instrumental in the origin of species. Now, Albertson and colleagues present evidence that transgressive

segregation and genetic covariation of functionally related traits could have contributed to the explosive adaptive radiation of East African cichlid fishes [4,5].

Occurrence and causes of transgressive segregation

Rieseberg *et al.* [2] surveyed crosses between populations, inbred lines and closely related species of diverse animals, including a liver fluke, crustaceans, insects, teleost fishes, salamanders, frogs, lizards, birds and mammals, and several species of monocot and dicot angiosperms. Ninety-one percent of these studies reported at least one transgressive trait, and 44% of all traits were transgressive. Transgressive segregation appeared to be associated with inbreeding and to be more common in plants than in animals, although, for plants, this might reflect inbreeding. Diverse traits exhibit transgressive segregation, and they could contribute to ecological divergence and reproductive isolation between hybrids and parental species.

Rieseberg *et al.* [2] considered several possible genetic causes for transgressive segregation in hybrids. Apart from complementation among loci (Box 1), other possible causes are mechanistically implausible or can only account for a small fraction of cases. Their compilation indicated that transgressive segregation results from interactions among loci with alleles that have opposing effects on phenotypes within each parental species but could have reinforcing effects (i.e. complementation) in hybrid generations after the F1 generation. Albertson and colleagues [4,5] investigated the genetic basis for the evolutionary diversification of feeding (trophic) structures

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Box 1. How are transgressive phenotypes produced?

Transgressive segregation is the production of F₂, backcross, or later-generation hybrid progeny with phenotypes that can fall outside the phenotypic range of the parental populations or species from which they were derived [2]. Transgressive phenotypes can be produced when alleles at multiple loci that originated in different parental populations recombine in the hybrids. This paradoxical expansion of phenotypic variation beyond the range of both parental populations depends upon the existence at some loci of alleles that increase the value of the phenotype and of alleles at other loci that reduce its value within each of the hybridizing parental populations. Consequently, alleles at different loci cancel each other out, limiting the range of phenotypes within each parental population. If the interactions among alleles at these loci are largely additive, and alleles at some homologous loci in the two parental populations have opposite effects on the value of the phenotype, hybrids can have transgressive phenotypes.

Consider a simple hypothetical example (Table I), in which each allele at four unlinked loci increases or decreases the score of a phenotype by one unit. In this example, both parental populations (or species) have a fixed allele (+1 or -1) at each locus, but alleles at loci A and B counteract the effects of alleles at C and D, producing net scores that sum to zero within each parental population. For example, the genotypic scores at loci A, B, C, and D in Population I are +2, +2, -2, -2, respectively, which add up to zero. F₁ hybrids also have a net score of zero, but their score results from heterozygosity for alleles with equal and opposite effects, +1 or -1, at all four loci. The genotypic scores in all F₁ hybrids at loci A, B, C, and D, will be +0 +0 +0 +0, respectively, which also add up to zero. However, F₁ hybrids have genotypes that can contribute -4, -2, 0, +2 or +4 units to the net score of a gamete. Consequently, the net scores of F₂ hybrid zygotes can be from -8 to +8, with intermediate scores at intervals of two units. In reality, effects at other loci and environmental variation would also contribute to differences between populations I and II and their F₁ and F₂ hybrids. If transgressive phenotypes of the F₂ hybrids promote ecological divergence and reproductive isolation, transgressive segregation can be a key genotypic innovation for adaptive radiation.

Table I. Hypothetical example of transgressive segregation involving four-locus, two-allele genotypes in two parental populations and their hybrid descendants

Locus	Popu- lation I	Popu- lation II	F1 Hybrid	F2 Hybrid
A	+1, +1	-1, -1	+1, -1	+1, +1; +1, -1; -1, -1
B	+1, +1	-1, -1	+1, -1	+1, +1; +1, -1; -1, -1
C	-1, -1	+1, +1	+1, -1	+1, +1; +1, -1; -1, -1
D	-1, -1	+1, +1	+1, -1	+1, +1; +1, -1; -1, -1
Net score	0	0	0	+8, +6, +4, +2, 0, -2, -4, -6, -8

in East African cichlid fishes. They carried out linkage mapping of morphometric traits in interspecific F₂ hybrids and demonstrated the potential for transgressive segregation and genetic covariance to facilitate endemic radiation.

Genetic architecture in cichlids

Albertson and colleagues [4] studied two closely related but morphologically and ecologically divergent species of Lake Malawi cichlids. *Labeotropheus fuelleborni* uses its ventrally directed mouth to bite algae off the substratum, whereas *Metriaclima zebra* sucks plankton from the water with its narrow, terminal mouth. The authors used geometric morphometrics (see [6,7]) to estimate the shape of the jaws, skull and other trophic structures in the head of the parental species and their F₁ and F₂

hybrids, which had all been reared under common laboratory conditions. They used 137 microsatellite or RFLP markers in the F₂ hybrids to generate a linkage map that identified chromosomal regions that have significant associations with shape variables [4].

A larger proportion of the variation than expected by chance for the oral jaw apparatus and dentition maps to a limited set of chromosomal regions, indicating that pleiotropic genes that influence multiple traits or separate but tightly linked genes are located within these regions. Eight chromosomal regions affected multiple trophic traits, including one on linkage group (LG) 16 that influences tooth, lower jaw, and skull shape, and another on LG2 that affects lower jaw length and depth. Genes that affect both upper and lower jaw variables map to LG1, 2, 10 and 16. Bone morphogenic protein 4 (*Bmp4*) also maps to the same chromosomal interval of LG2, suggesting that it is a pleiotropic gene that influences multi-trait variation. Thus, even in interspecific hybrids, these trophic traits will tend to vary in concert among progeny, conserving their functional relationships (e.g. see [3,8]).

Albertson and Kocher [5] performed a principal component analysis (PCA) of shape variables from the lower jaw and neurocranium using the pure-bred and hybrid progeny from their previous study [4] plus a small laboratory-reared sample of *Pseudotropheus tropheops*. PCA incorporates multivariate data into synthetic variables that can be used to represent a large proportion of the variation in a data set. The first two axes of the PCA accounted for 70% of the variation of both jaw and skull shape (Figure 1). For lower jaw shape, the parental species were divergent for PC1 but similar for PC2. Their F₁ and F₂ hybrids were intermediate to the parental species along PC1 and similar to both parental species along PC2. For skull shape, the parental species differed slightly along PC1 and strongly along PC2. Both the F₁ and F₂ progeny were intermediate to the parental species along PC2 (although the F₁s were closer to *M. zebra*). The F₁ progeny were also distributed within the range of parental phenotypes along PC1. However, the distribution of F₂ phenotypes along PC1 extended to lower values than did either parental form, exhibiting transgressive segregation. Notably, specimens of *P. tropheops* fell within the range of F₂ hybrids between *L. fuelleborni* and *M. zebra* and outside the range of phenotypes for either parental species. Thus, transgressive skull-shape phenotypes in the F₂ progeny resemble the phenotype of another species of Lake Malawi cichlid.

These results illustrate the potential for genes with counteracting effects in parental species to generate phenotypic novelty in their F₂ hybrids by transgressive segregation [2]. Jaw shape differences between *L. fuelleborni* and *M. zebra* map to 21 loci, only one of which has effects that are antagonistic to those of other loci for jaw shape in the parental species [4]. Transgressive segregation did not occur in jaw shape. Albertson and Kocher [5] attributed consistent phenotypic effects among loci that affect non-transgressive traits to recent, strong, directional selection in opposite directions in the parental species. By contrast, differences in skull shape map to four

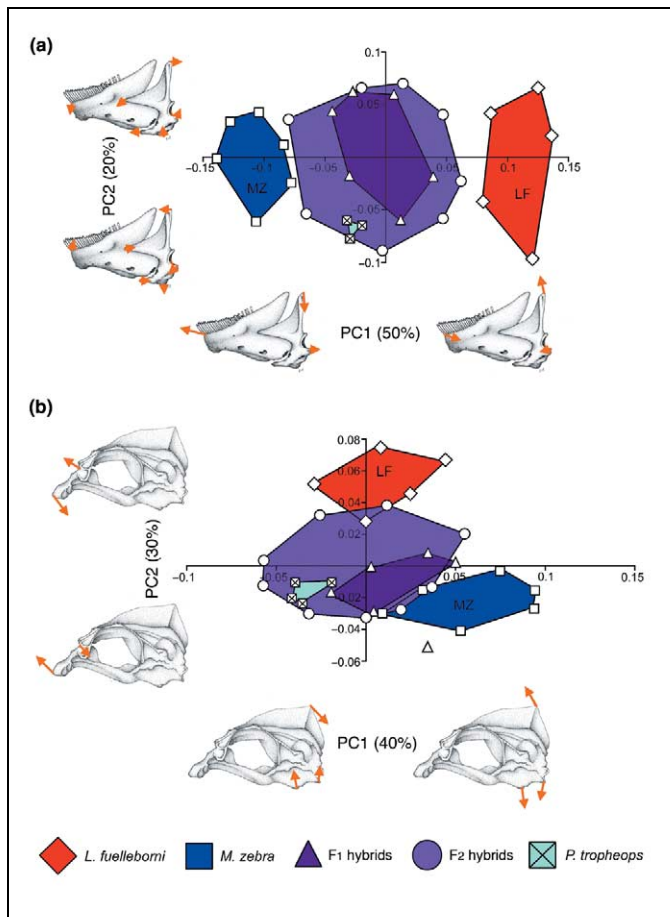


Figure 1. Distribution of jaw and skull-shape variables in pure-bred and hybrid cichlid progeny. Shaded areas represent the bivariate distributions of shape variables for each sample along the first two principal component (PC) axes. Percentages in parentheses indicate the proportion of shape variation explained by each PC. Jaw and skull illustrations are their shapes at the origin of the PC axes, and arrows show the directions and (150% exaggerated) magnitudes of shape differences at the point on the bone where each arrow is rooted for specimens at the extremes of PC1 and PC2. (a) Jaw shape. *Labeotropheus fueleborni* (LF) and *Metriaclima zebra* (MZ) differ along PC1, which represents variation in the length and height of the lower jaw. Samples from hybrids and *Pseudotropheus tropheops* are intermediate to the parental species along PC1. Hybrid populations are not transgressive along PC2, which represents shape variation throughout the lower jaw. (b) Skull shape. *L. fueleborni* and *M. zebra* partly overlap along PC1, which represents variation in the posterior neurocranium, but are separate along PC2, which represents variation in the anterior neurocranium. Transgressive segregation occurs in the F2 hybrids, because their minimal values are lower (expanded to the left) than those of both parental species along PC1, but they are not transgressive along PC2. The *P. tropheops* sample is located within the lower-left portion of the distribution for F2 hybrids and near the limit of the distribution for *L. fueleborni* along PC1. Modified, with permission, from [5].

loci that form two pairs with counteracting effects in each parental species. The authors attributed counteracting effects among loci within species to recent stabilizing selection and drift (see [9]). Hybrid phenotypes in which transgressive segregation and strong genetic covariance occur can be both novel and morphologically integrated [8]. Rieseberg *et al.* [2] reported several studies in which complementation among loci could explain transgressive phenotypes, and Albertson and Kocher's [5] results show that this mechanism could have had an important role in the adaptive radiation of East African cichlids.

Hybridization and adaptive radiation

Hybridization can either retard or promote evolutionary diversification, but its retarding effects have generally been emphasized [10]. Hybridization between divergent sympatric species should reduce divergence between them, possibly leading to their complete integration. Similarly, gene flow between divergent parapatric and allopatric populations will tend to reduce differences between them.

However, emigrants from a divergent population might also contribute novel genetic variation to the recipient population, increasing its potential to respond to directional selection [11–13]. The importance of allopolyploidy (genomic duplication owing to interspecific hybridization) for plant speciation has long been appreciated [14]. Seehausen [1] proposed that hybrid swarms involving closely related species increase variation that forms the basis for further divergence. Closely related species will tend to produce viable, fertile hybrids, and they might have transgressive phenotypes that are adapted to exploit underutilized ecological resources. If the hybrid phenotypes also exhibit morphological integration, their potential to form new species will be enhanced.

Adaptive radiation has traditionally been attributed to ecological opportunity, having key phenotypic innovations or a combination of these factors [15]. However, Rieseberg *et al.* [2] and Seehausen [1] emphasized the potential for transgressive segregation, which depends on hybridization and strictly genotypic innovations, to contribute to evolutionary diversification. Genetic covariation of functionally related traits represents another strictly genotypic innovation that might also increase the potential for hybrids to diverge phenotypically and found new species [4]. The East African lake cichlids have long been recognized as a set of large, relatively young, endemic radiations [16,17]. Similar to other major radiations, speculation about the causes of their diversification has focused on ecological opportunity and key phenotypic innovations [18,19]. Several recent studies indicate that some cichlid species were founded by interspecific hybrids (see references in [1,5]), and now Albertson and colleagues [4,5] have provided evidence that transgressive segregation and genetic covariation are key genetic innovations that rival ecological opportunity and phenotypic innovation as the keys to adaptive radiation.

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Letters

Organisms in nature as a central focus for biology

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In his recent discussion in *TREE* [1], Greene eloquently and effectively describes the value of natural history, the study of organisms in their natural environment. As he noted, natural history is the reason why many of us became scientists, and is also the basis for widespread human interest in biology. Opportunities for biological conservation and future funding for biology rely on maintaining that strong human interest.

I agree with all of Greene's points except his suggestion that the best hope for funding natural history is the private sector of society. He feels that governments are unlikely to underwrite the exploration of biodiversity on a large-enough scale. Although certainly reflective of the current situation, this argument seems unnecessarily pessimistic. Governments should provide funding for the very reasons outlined in his article.

As a recent program officer for the US National Science Foundation (NSF), I can say with confidence that the NSF does respond to the wishes of the scientific community, if they are clearly stated. The Biodiversity Surveys and Inventories Program of the NSF received an increase of US\$10 million in 2003 in response to the consensus among taxonomists that inventories of species-level diversity must be dramatically increased. This initiative, 'Planetary Biodiversity Inventories' (PBI), was a direct response to clearly stated concerns from the scientific community that too little funding was going to the Biodiversity Surveys and Inventories Program.

Unfortunately, no plan for a second PBI seems to be in place, perhaps because the NSF is not hearing from

natural historians that such funding is a priority. It should be self-evident, given that 37 proposals were received and only four were funded, but perhaps it is more evident that squeaky wheels get the grease, and we natural historians are not squeaking loud enough.

We should not accept the current funding priorities at NSF. It is obvious to all that much of the biodiversity on Earth is rapidly disappearing. As the human population passes the 6 billion mark and makes increasing demands on natural resources, other species are disappearing at an increasing rate. Already, we have lost a large amount of information about native distributions and natural demographic patterns. Soon, all information about a substantial portion of species-level diversity will also be lost before it is even known.

The paltry funding available from governmental agencies, including the NSF, for documenting biodiversity is unacceptable. The annual budget at the NSF for the Biodiversity Surveys and Inventories Program is ~US\$10 million, and that for the Biological Research Collections Program only ~US\$6 million. Other programs, particularly those with a molecular orientation, are much better funded; for example, the Plant Genome Research Program receives ~US\$80 million–100 million per annum (and estimates that US\$1.3 billion will be needed to meet its objectives). Surely, documenting the diversity of the planet, and reaping the huge amount of useful information contained therein, is as important as understanding the plant genome.

All organismal biologists need to make their collective voice heard. We owe it to science, and we must do it to achieve a goal that cannot wait: to identify the best areas

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