

Hybridization, speciation and evolutionary biology

Dr. Sean Hoban



Overview of topics

- **What is hybridization**
- What are some examples?
- History of hybridization, **some early questions**
- How does it fit into **species concept**
- What are the **genetic mechanisms** of hybridization
- How common is it?
- What are its **ecological and evolutionary importance**
- New theories
- Hybridization and **conservation** of rare species

Important terms: hybridization, F1, backcross, introgression, hybrid zone, epistasis, transgressive segregation, unidirectional hybridization, cytonuclear interaction, adaptive radiation

Hybridization is defined as “the interbreeding of individuals from two species, populations, or groups of populations, which are distinguishable on the basis of one or more heritable characters”

Introgression is “the permanent incorporation of genes from one set of differentiated populations into another... the incorporation of alien genes into a reproductively integrated population system”

A **hybrid taxon (hybrid species)** is an independently evolving, **historically stable** population or group of populations possessing a unique combination of heritable characteristics derived from interbreeding of representatives from two or more discrete units (e.g. races, subspecies, species, etc). Historical stability implies that the mosaic of characters inherited from independent lineages is retained in the population, passed on from parent to offspring.

Definition of **hybrid taxa** is difficult... selection of criteria for placing groups into specific taxonomic categories (e.g. subspecies, species, genera)

Platanus × acerifolia
London planetree

hybrid of *Platanus orientalis* (oriental plane) and the
Platanus occidentalis (American sycamore)



How common?

At least 25% of plant species and 10% of animal species, mostly the youngest species, are involved in hybridization and potential introgression with other species. (rarity on a per individual basis, but common on a per species basis. Although hybrids are rare in populations, a few hybrids can provide a bridge)

Natural hybrids also are **unevenly distributed taxonomically...** concentrated in a small fraction of families and genera... phylogenetic hotspots... characteristics significantly associated with these hybridizing genera include perennial habit, outcrossing breeding systems, and asexual reproductive modes that allow stabilization of hybrid reproduction.



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HYBRIDIZATION OF THE HABITAT

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In a surprising number of cases the **experimental evidence shows that the species can be crossed readily, in the breeding plot**, but no hybrids appear under natural conditions. In many cases which have been carefully investigated, **hybrids, though usually rare, do occasionally occur but leave no apparent descendants except under unusual conditions**. This experimental evidence, such as it is, justifies the generalization that **species maintain themselves as recognizable units** even where they are interfertile and even when there is a considerable opportunity for them to hybridize.

Why should this be so? (Besides inherent isolating mechanisms)

- ❖ The **first hybrid generation is intermediate** between the parents and is as uniform as they are, or even more so. It is usually more vigorous than either and more robust in nature.
- ❖ The **second hybrid generation**, while on the average intermediate, **is extremely variable**. Usually no two individuals are alike. The variation is usually bewildering, but it can be shown to have a general trend from a few individuals more or less like one of the parental species, to a great bulk more or less like the first-generation hybrid...
- ❖ The first **backcross is made up largely of plants which resemble the species to which they have been backcrossed**. If we take one of these and cross it back a second time to the same parent... the seedlings resemble this species very much indeed...

The chief result of hybridization under such conditions is the **enrichment of variation in the participating species... introgressive hybridization... a means by which elements in the germplasm of one species might introgress into the germplasm of the other.**

Such hybridization is cryptic and only by very specialized techniques can we measure its exact importance.... gene flow from one species to another may go far beyond any point which could be detected by ordinary morphological techniques.

Introgression therefore gives us a partial answer to our original question as to why hybrids are so seldom met with in nature. It is because when hybrids do occur, they usually perpetuate themselves, if at all, in backcrosses to one or the other parental species and the mongrel nature of their descendants is not apparent. The commonest result of hybridization is introgression, and introgression must be excessive before it will produce results conspicuous enough to impress biologists who are not making a deliberate search. This is only half an answer. Why do interfertile species limit themselves very largely to backcrosses when they meet under natural conditions...

The effect of the habitat is important.

The argument: it is now known that the **physiological differences between species segregate in the same way as do the morphological ones**... segregation and recombination of such physiological differences as length of blooming season, resistance to diseases, resistance to cold, light tolerance, etc. If, therefore, we cross two species differing in their **ecological requirements** we may expect these physiological differences to segregate as follows : The first hybrid generation will be uniform... and on the whole they will be for conditions intermediate between those required for the two parents. **The second generation will be made up of individuals each of which will require its own peculiar habitat.**

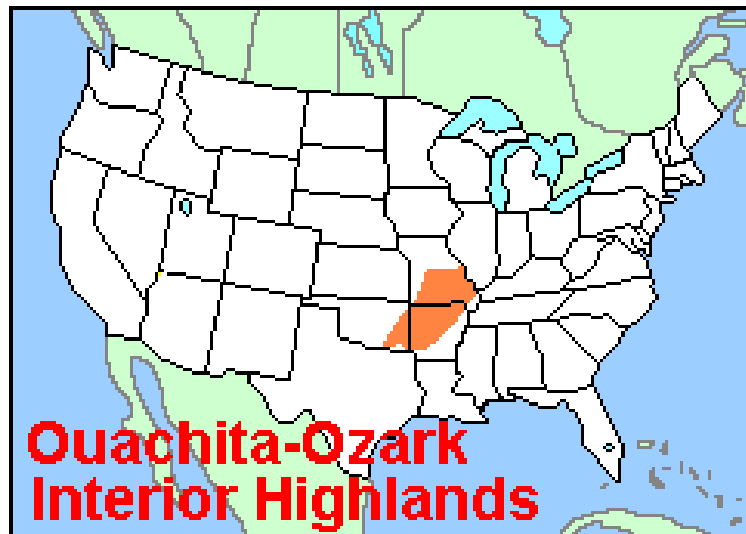
In nature therefore **we might reasonably expect to find first generation hybrids growing in an intermediate zone...** **The persistence of the various second generation recombinations would require a habitat seldom or never met with**, where various combinations of the two parental habitats are found in close juxtaposition.

***Tradescantia subaspea* and *T. canalicztlata* in the Ozark Plateau.**

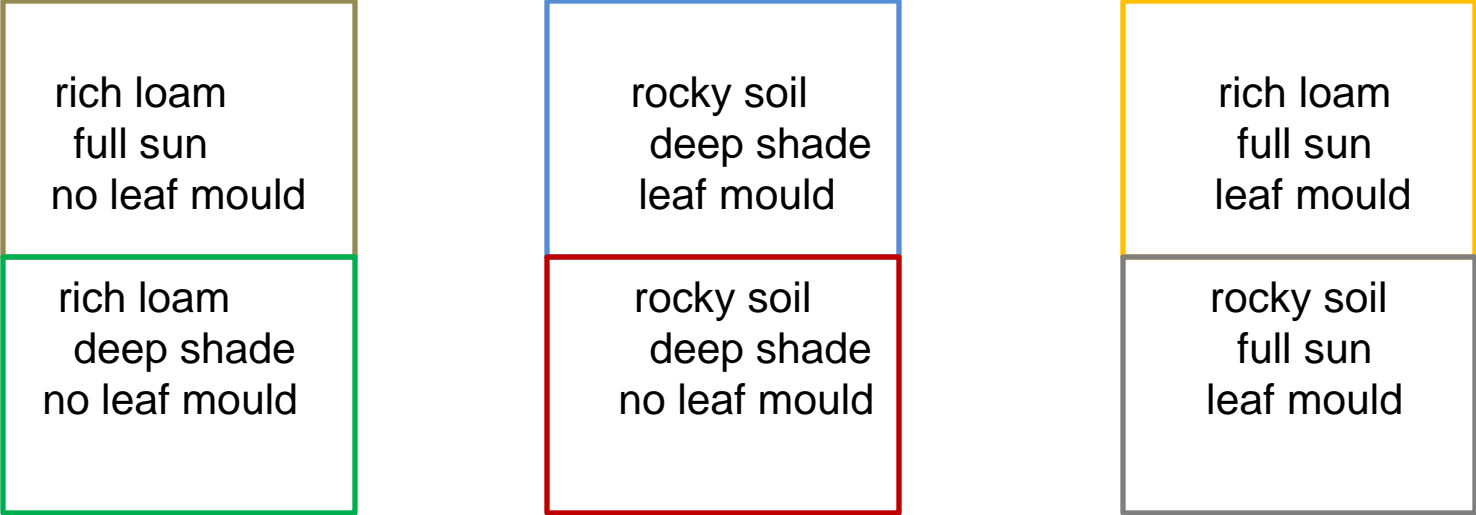
The former grows in deep rich woods at the foot of bluffs while the latter grows up in full sun at the edge of the cliffs:

rich loam
deep shade
leaf mould cover

rocky soil
full sun
no leaf mould cover



would require the following **six new habitats in addition to the parental ones** (these six represent only the extreme recombinations; a whole series of intermediates will also be required) :



generally recognized that if hybrids are to survive we must have intermediate habitats for them. It has not been emphasized, however, that if anything beyond the first hybrid generation is to pull through, **we must have habitats that are not only intermediate but which present recombinations of the contrasting differences of the original habitats.**

If the two species differ in their response to light, soil, and moisture (and what related species do not?) we must have **varied recombinations of light, soil, and moisture** to grow their hybrid descendants. Only by **a hybridization of the habitat** can the hybrid recombinations be preserved

The number of different kinds of habitats required by the hybrids will rise exponentially with the number of basic differences between the species. With **ten such differences, around a thousand different kinds of habitat would be needed** to permit the various recombinations to find a niche somewhere as well suited to them as the original adjacent habitats were to the two parental species. Under natural conditions anything like such a situation is close to impossible. **Ordinarily it is only through the intervention of man that it is even remotely approached.** Even in these cases the new "Recombination Habitats" will largely be limited **to habitats pretty much like those required by one of the parental species, but which in a few characteristics approach the requirements of the other parent.**

on the Mississippi delta, a series of long, narrow farms run straight back from the highway side by side, almost the precision of experimental plots.

The original environment at that point was fairly uniform, **but each man has treated his farm a little differently... the numbers and kinds of hybrids varied from farm to farm.** Some had few or none, while others, even when adjacent, had hybrids in great quantities; there were significantly more of them where the meadows had been pastured. one farm in particular... had been repeatedly cut over and had in addition been heavily pastured. It had a swarm of different hybrid derivatives, almost like an experimental garden

Mississippi River Drainage Basin



Does this mean that introgression as a phenomenon is limited to the areas disturbed by man and that its results are mere artifacts and not genuine natural phenomena?

I believe that **at particular times, and in particular places, introgression may have been a general evolutionary factor of real importance...** For instance when **newly colonizable areas** emerged from the sea or when various floras spread out onto the northern lands denuded by Pleistocene glaciations.

1. Along the coast of California there are **peninsulas which once were isolated islands** but which are now united with the main land...
2. Peninsular Florida... During parts of the Tertiary it was an **island or group of islands which finally became attached to the mainland**. Species and varieties which became differentiated during the glacial period must then have had opportunities to hybridize with their relatives on the mainland.

... at such a time related species in many genera might have met and hybridized under **conditions where competition would not have been keen and where associations of plants were in the making instead of already existing as tightly closed corporations...** an area conducive to the survival of some of the hybrid recombinants



1. Experimental evidence shows that sterility will not account for the rarity of hybrids under natural conditions.
2. Natural hybridization is largely limited to backcrosses which resemble the parental species so closely that special methods are required to detect them readily.
3. One of the factors limiting hybridization to such introgression is imposed by the habitat for the following reason: **Two species differing in their habitat requirements will produce a first generation hybrid adjusted to a uniform intermediate environment. The second generation however consists of individuals each of which requires its own peculiar habitat for optimum development.** Such heterogeneous habitats are seldom or never met with.
4. It is concluded that hybrid swarms can survive only in "hybridized habitats." While most of the latter result from humans, similar **conditions have prevailed in pre-human times when new lands were opened up to colonization by diverse floras.** At such times and places introgressive hybridization must have played an important role in evolution

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A TAXONOMIST'S EXPERIENCE WITH HYBRIDS IN THE WILD¹

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the taxonomist is **accustomed to think of the species in certain groups as clear cut and easy to work with, while other groups are difficult and the species more or less confused with no sharp boundaries.**

...between certain species a great burst of **crossing may occur locally all at once, and that this may or may not continue thereafter for a period of time.** Over a limited area one will often find abundant hybrid individuals showing all manner of combinations of the characters of two parent species. The lay botanists get the impression that here the genus is "running wild." Elsewhere over large areas, even miles in extent, there may be no evidence of crossing whatever.

But **what causes plants to hybridize thus locally and suddenly?** ...the environment has **something to do with the matter**... In Newfoundland a railway crosses the island. **Near the railway the forest has been largely destroyed by fire or through logging operations.** Tracts miles in extent are covered with dead brush and dense scattered thickets of scrub growth. Amelanchier is common in this region... taxonomically it was found to be a mess, as almost every individual seemed different from its neighbor. **In less disturbed areas the plants were more uniform... it appeared that many of the plants in the disturbed areas were hybrids,**

on the Blue Hills south of Boston, the forest has largely disappeared. Frequent fires have ravaged the region, and when visited several years ago presented **alternating areas of bare rock, brush and open thicket.** Amelanchiers were common, but few individuals were like any known species or like each other...aberrant forms were **hybrids of three species** occurring in the neighborhood, of which **two were dry ground species and one an inhabitant of the swamps**



Finding conspecific mates

Hybrids in the field then tend to occur locally at some particular time and often in considerable abundance. While the cause of this is still obscure, a very suggestive hypothesis would connect it directly with the disturbed conditions just mentioned. It might well be that these conditions induce irregularities in the time of flowering. If some flowers are produced earlier or later than the normal period for that species, then these **flowers might find no pollen from their own species but only that from some other species** whose flowering period was earlier or later, as the case might be.

As to the **significance in evolution** and in the species question of this hybridization in the wild... two generally accepted sources of divergence between parent and offspring, namely, **gene mutation and hybridity**.

...whether **hybridity**, which combines the genes of two parents, **could produce new characters often enough and of sufficient magnitude to account for the great morphological diversity in plants**. It is clear, I think, that we have not yet solved the problem of the origin of species.

Another serious difficulty in the way, if we are to consider hybridity as an important cause in the origin of species, **is the dearth of evidence that it operates in nature**. The hybrids seem like swarms of bees, buzzing around for a time, only to disappear, leaving the fundamental species to continue.

What, then, becomes of the hybrids that from the standpoint of geological time are being produced in hordes? This to me is one of the interesting problems in evolution, second only to the problem of the origin of species in the first place...

I can not help but see difference between the temporary hybrid and the fundamental established species reaching back perhaps to the glacial epoch or beyond... As pointed out, **the mass of hybrids in the cases under observation seem ...in no way to affect the fundamental species**

GENETICS AND THE FITNESS OF HYBRIDS

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Key Words adaptation, epistasis, hybridization, speciation, transgressive segregation

■ **Abstract** Over the years, the evolutionary importance of natural hybridization has been a contentious issue. At one extreme is the relatively common view of hybridization as an evolutionarily unimportant process. A less common perspective, but one that has gained support over the past decade, is that of hybridization as a relatively widespread and potentially creative evolutionary process. Indeed, studies documenting the production of hybrid genotypes exhibiting a wide range of fitnesses have become increasingly common. In this review, we examine the genetic basis of such variation in hybrid fitness. In particular, we assess the genetic architecture of hybrid inferiority (both sterility and inviability). We then extend our discussion to the genetic basis of increased fitness in certain hybrid genotypes. The available evidence argues that hybrid inferiority is the result of widespread negative epistasis in a hybrid genetic background. In contrast, increased hybrid fitness can be most readily explained through the segregation of additive genetic factors, with epistasis playing a more limited role.

the historically common view of natural hybridization as **an evolutionarily unimportant process**. This view is largely based on the observation that crosses between divergent lineages often give rise to progeny with decreased levels of viability and/or fertility

When hybridization has been directly implicated in the evolutionary process, it has **traditionally been for the role it may play in finalizing speciation**. Hybrid zones, therefore, have generally been viewed as transient, **with selection on mating preferences ultimately giving rise to “good” species** or, if stable, as little more than an impediment to continuing divergence.

A less common viewpoint is that of hybridization as a relatively widespread and potentially creative evolutionary process. Indeed, introgression (the transfer of genetic material from one species into another via hybridization) has been documented in a wide variety of both plant and animal taxa.

In later generations, **one possible outcome of such heterosis would be the introgression of favorable alleles from one parental population into the other**... the introgression of certain chromosomal blocks from one taxon into another.

Alternatively, if the hybrid offspring are isolated in some way from their parents, the joint effects of recombination and natural selection may decrease the frequency of deleterious alleles, ultimately giving rise to a **true-breeding hybrid lineage** with increased fitness relative to its parents

exogenous selection is believed to play a central role in the establishment of relatively fit hybrids. The main reason for this is that, in the absence of niche differentiation, new hybrid genotypes are likely to be overwhelmed by competition and/or gene flow from the parental populations...

Major Ecological Transitions in Wild Sunflowers Facilitated by Hybridization

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Helianthus ... three species that appear to be derived via this mode: *H. anomalus*, *H. deserticola*, and *H. paradoxus*... all three species appear to be derived from the same two parents (*H. annuus* and *H. petiolaris*) as they combine parental allozymes and share the chloroplast DNA (cpDNA) haplotype of one or both parental species... the three hybrids have a haploid chromosome number of 17.

They differ from the parental species, however, in terms of **geographic distribution and habitat preferences**. *Helianthus paradoxus* is endemic to saline brackish marshes in west Texas, whereas *H. anomalus* and *H. deserticola* are xeric species restricted to the Great Basin desert of the southwestern United States... the parental species are widespread throughout, with *H. annuus* found primarily in mesic soils and *H. petiolaris* in dry, sandy soils.

THE RATE OF GENOME STABILIZATION IN HOMOPLOID HYBRID SPECIES

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Homoploid hybrid speciation has been recognized for its potential rapid completion, an idea that has received support from experimental and modeling studies. Following initial hybridization, the genomes of parental species recombine and junctions between chromosomal blocks of different parental origin leave a record of recombination and the time period before homogenization of the derived genome. We use detailed genetic maps of three hybrid species of sunflowers and models to estimate the time required for the stabilization of the new hybrid genome. In contrast to previous estimates of 60 or fewer generations, we find that the genomes of three hybrid sunflower species were not stabilized for hundreds of generations. These results are reconciled with previous research by recognizing that the stabilization of a hybrid species' genome is not synonymous with hybrid speciation. Segregating factors that contribute to initial ecological or intrinsic genetic isolation may become stabilized quickly. The remainder of the genome likely becomes stabilized over a longer time interval, with recombination and drift dictating the contributions of the parental genomes. Our modeling of genome stabilization provides an upper bound for the time interval for reproductive isolation to be established and confirms the rapid nature of homoploid hybrid speciation.

Transfer of useful traits via introgression

Novel hybrids may present a problem for biological control programs using highly host-specific agents. Some genotypes of biological control targets have been found to have differential susceptibility to fungal or insect control agents. If a biological control agent is effective against some invasive types but not others, there is potential for the uncontrolled types to increase their range, as happened with ecotypes of *Chondrilla juncea* L..

Recent efforts at classical biological control of saltcedar in the western USA have resulted in the field release of **a leaf-feeding chrysomelid beetle, *Diorhabda elongata*, which has established and extensively defoliated saltcedar at some sites but failed to establish at other sites**. This indicates that there are gaps in our knowledge about saltcedar, *Diorhabda*, or the ecology of their interactions in the USA.

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ORIGINAL PAPER

Introgression between invasive saltcedars (*Tamarix chinensis* and *T. ramosissima*) in the USA

John F. Gaskin · David J. Kazmer

The **creative potential of natural hybridization depends critically on the production of recombinant genotypes that can outperform their parents in at least some habitats**. Broadly speaking, hybrid fitness can be influenced by either endogenous or exogenous selection.

- **Endogenous selection** refers to that which acts against certain hybrid genotypes regardless of the environment in which they occur... inherent loss of fitness is assumed to result from either meiotic irregularities or physiological/ developmental abnormalities in individuals of mixed ancestry (hybrid incompatibility).
- **Exogenous selection**, on the other hand, refers to environment-specific fitness differences... the distribution of genotypes across a hybrid zone is assumed to be governed by adaptation to different habitats... many hybrid genotypes fail to find suitable habitat, (but some) recombinant genotypes outperform parents in certain habitats

Indeed, recent theoretical work confirms that **a small fraction of hybrid genotypes will likely outperform their parents, even in parental habitats**. (species not perfectly adapted)

We no longer need to ask whether or not hybrids will exhibit a wide range of fitnesses. They do. Of greater interest are the mechanisms underlying such fitness variation. As pointed out elsewhere, **the outcome of hybridization depends not only on the distribution of hybrid fitness, but also on the underlying genetics**

The role of epistasis in adaptive evolution...

As a result of the highly integrated nature of the genome, selection may lead to the production of what Dobzhansky has termed **“coadapted” gene complexes**.

In contrast, Fisher argued that natural selection acts primarily on **single genes**, rather than on gene complexes.

hybrid incompatibility, is fully consistent with both the Wrightian and Fisherian worldviews... because hybridization produces **a vast array of recombinant genotypes that have never before been subjected to selection** (together). On average, these genotypes will be less well adapted than their parents, giving rise to selection against hybrids.

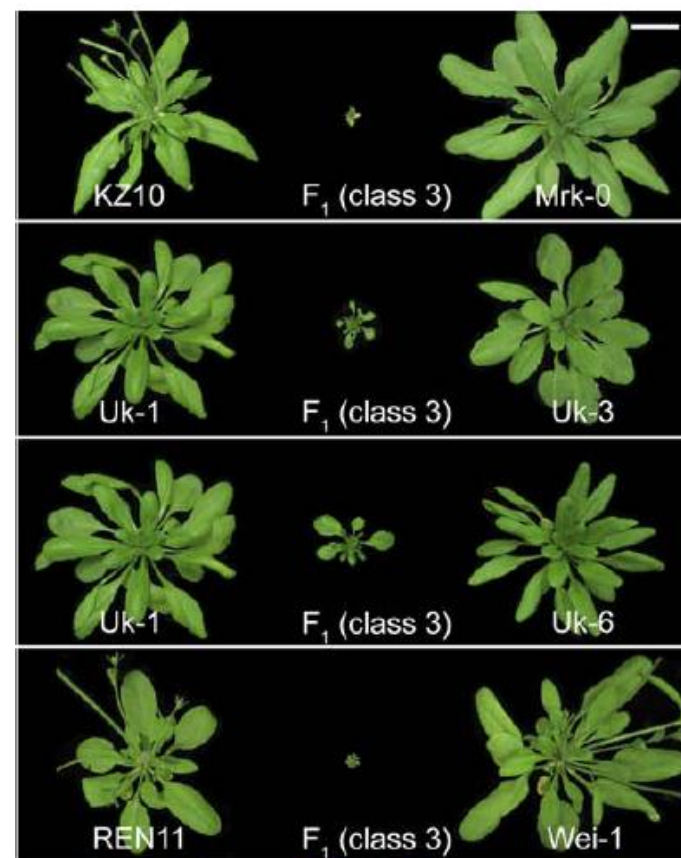
Bateson-Dobzhansky-Muller (BDM) model assumes that an ancestral population consisting solely of individuals of the genotype aa/bb is broken into two parts that are temporarily isolated from each other. In one subpopulation, a new allele (A) is then assumed to arise at the first locus. Meanwhile, a new allele (B) is assumed to arise in the other subpopulation. the interaction of A with B is assumed to produce some sort of developmental or physiological breakdown, such that hybridization leads to the production of offspring with decreased levels of viability and/or fertility.

similar interactions between one or more regions of the nuclear genome and some component of the cytoplasm (e.g., the chloroplast or mitochondrial genome) could also play an important role in hybrid incompatibility

Autoimmune Response as a Mechanism for a Dobzhansky-Muller-Type Incompatibility Syndrome in Plants

Kirsten Bomblies¹, Janne Lempe¹, Petra Epple², Norman Warthmann¹, Christa Lanz¹, Jeffery L. Dangl^{2,3,4}, Detlef Weigel^{1*}

Epistatic interactions between genes are a major factor in evolution. Hybrid necrosis is an example of a deleterious phenotype caused by epistatic interactions that is observed in many intra- and interspecific plant hybrids. A large number of hybrid necrosis cases share phenotypic similarities, suggesting a common underlying mechanism across a wide range of plant species. Here, we report that approximately 2% of intraspecific crosses in *Arabidopsis thaliana* yield F₁ progeny that **express necrosis when grown under conditions typical of their natural habitats**. We show that several independent cases result from epistatic interactions that trigger autoimmune-like responses... **an allele of an NB-LRR disease resistance gene homolog is both necessary and sufficient for the induction of hybrid necrosis, when combined with a specific allele at a second locus**. Moreover, our finding that plant immune-system genes are involved in hybrid necrosis suggests that selective pressures related to **host-pathogen conflict might cause the evolution of gene flow barriers in plants**.



How many genes?

Introgression of *D. mauritiana* or *D. sechellia* chromosomes into the *D. simulans* genetic background.... results of this work indicate that **hybrid sterility results from a large number of genetic interactions**. Indeed, Palopoli & Wu estimate that there are at least **40 loci** that influence hybrid male sterility

H. petiolaris genomic regions introgress into the *H. annuus* background at rates lower than expected... result suggests that loci in these regions of the *H. petiolaris* genome interact unfavorably with some component of the *H. annuus* genome. there were **at least eight (possibly ten) *H. petiolaris* chromosomal regions** that introgressed at frequencies lower than expected. Analyses of hybrid fertility revealed a possible mechanism for this pattern: The majority of these underrepresented blocks were significantly associated with reduced **pollen fertility**.





The potential negative effect of **cytonuclear interactions** on hybrid viability
a significant excess of *I. fulva* alleles (and a deficit of *I. brevicaulis* alleles) in
one particular region of the genome on the *I. fulva* cytoplasmic background, but
not on the *I. brevicaulis* cytoplasmic background.

The **nonreciprocal nature of this deviation** suggests that hybridization has
disrupted favorable interactions between this region of the *I. fulva* nuclear
genome and some component of the *I. fulva* cytoplasm, leading to selection
against the *I. brevicaulis* genotype in this region... this result indicates the
possibility of hybrid incompatibility due to cytonuclear coadaptation.

How many genes?

hybrid sterility and inviability are predicted to evolve nonlinearly (i.e., faster) with respect to time. This “snowballing” effect could, therefore, lead to **an overestimate of the number of genes required for speciation**. What we do know is that the complex and widespread nature of these **incompatibilities makes them relatively effective barriers** to genetic exchange between taxa. Indeed, as the number of loci that contribute to reduced hybrid fitness increases, the likelihood of producing relatively fit hybrid genotypes decreases, and the proportion of the genome protected from gene flow increases.

In the absence of an extremely strong selective advantage, **epistatic selection** will be effective only during the first few generations following the onset of hybridization... hybrid founder events may play a critical role in the establishment of new hybrid lineages

Nonepistatic factors, on the other hand... Alleles that are favored regardless of genetic background will readily introgress across hybrid zones... such alleles can rapidly spread to fixation...additive effects of alleles segregating at complementary genes.

Evidence points to the importance of additive factors in the establishment and spread of favorable hybrid genotypes. However, the QTL mapping approaches generally employed in studies that have documented transgressive segregation **have low power for detecting epistasis**. Thus, epistasis may play a larger role in transgressive segregation than previously believed

Hybridization could lead to the production of individuals with unique character combinations (as suggested earlier). Because these ecologically isolated recombinants will be **more or less released from the competitive and swamping effects of close contact with their parents**, they will be free to evolve independently and, perhaps, develop some degree of reproductive isolation.

Hybrid Fitness

The creative potential of natural hybridization depends not only on the production of relatively fit hybrid genotypes, but also on the **genetic architecture of such hybrid superiority**. The importance of genetic architecture lies in **the likelihood of establishment and spread of favorable hybrid genotypes**.

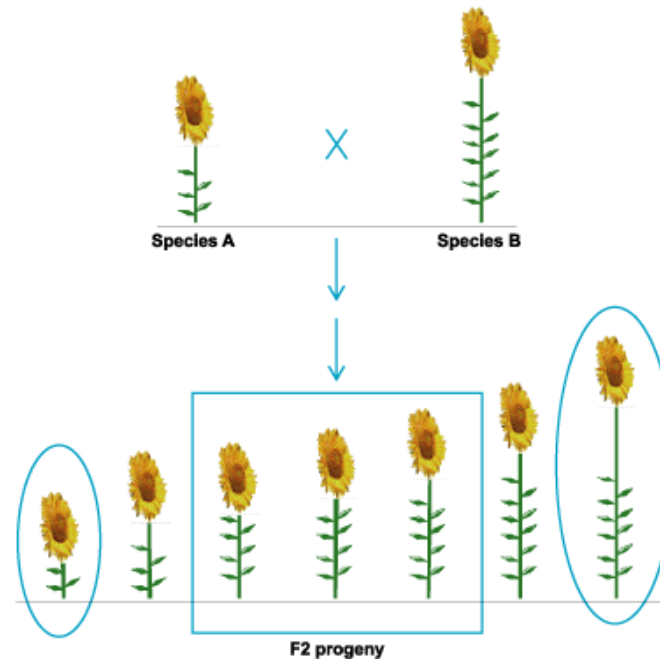
At a genetic level, increased hybrid fitness can arise in several ways. First generation hybrids often exhibit heterosis, or **hybrid vigor**, especially if their parents are inbred. Depending on the genetic basis of such heterosis, however, the increase in fitness **may be short-lived**, breaking down with the passing of Generations. In later generations, relatively fit hybrids may result from either the production of novel, favorably interacting (epistatic) gene combinations, or through the combining of advantageous alleles across noninteracting (additive) loci.

hybridization could give rise to genotypes that are intrinsically more fit than their parents. One mechanism by which this may occur is through the **purging of mutational load**. Due to the constraints of finite population size, mildly deleterious alleles can become fixed within lineages, leading to the gradual erosion of fitness (inbreeding depression). Hybridization between lineages could, therefore, lead to the production of heterotic F1 hybrids due to the masking of deleterious recessive alleles.

Because of the emphasis placed on niche divergence by many students of hybridization, the potential for the production of relatively fit hybrids is often tied to the production of novel or extreme hybrid phenotypes out, such as **transgressive segregation** appears to occur frequently in crosses between divergent lineages in both plants and animals traits such as fecundity, as well as tolerance to various biotic and abiotic stresses

...usually due to segregation variance. Segregation variance is caused by the **complementary action of different genetic loci** that are fixed for alleles with effects in opposite directions in the parent species and that have additive effects when recombined in their hybrids (e.g. alleles with opposing sign on quantitative trait loci).

Helianthus sunflower species combine additive effects of different parental loci for **salt tolerance**, enabling them to colonize habitats in which neither parent taxon performs well. Interspecific hybrids in *Xenopus* frogs combine specific **parasite resistances** of both parents but express susceptibility to a third parasite that both parents are resistant to.



When considering the evolutionary importance of natural hybridization, we are thus faced with an odd **dichotomy**. On the one hand, there is a substantial body of evidence documenting that, in the majority of cases, hybrid matings give rise to progeny with decreased levels of fertility and/or viability. In fact, along with various prezygotic barriers to hybridization, this sort of reproductive isolation is the very reason why we have distinct species. On the other hand, there are numerous examples of potentially adaptive introgression, as well as the production of new hybrid species

...underscores a fundamental aspect of the evolutionary process, namely the overwhelming importance of rare events.

Indeed, it is widely recognized that **evolution proceeds as a direct consequence of extremely rare events—the occurrence of beneficial mutations, long-distance migration, founder events, etc.**,—yet, with reference to the production of relatively fit hybrid genotypes, it has been argued that the rarity of such individuals precludes an important role for hybridization in evolution. Barton has gone on **to argue that, in abundant species, mutation is not limiting and favored variants are therefore more likely to arise via mutation than hybridization.**

What this view neglects to recognize is that such mutations may arise anywhere within the range of a species, but may only be favored in certain locales. Although the same might be said of novel variants resulting from hybridization, **hybrid matings often occur near the edge of a species range or in marginal habitats—just the sort of places where new variants may be most likely to survive and thrive.** In contrast to mutation, which will occur at the same low rate across the range of a species, hybridization provides a mechanism by which genetic variation can be generated in areas where the resulting variants are most likely to invade and utilize novel habitats.

We have now entered a new phase of research on natural hybridization. Instead of focusing on this process as an impediment to “normal” divergence, or as an evolutionary epiphenomenon, **numerous investigators are approaching their studies assuming that natural hybridization can be evolutionarily important in its own right.** Indeed, the future is bright for studies of natural hybridization. The tools required for detailed genetic analyses are widely available, and there is now a freedom to investigate previously discounted questions and hypotheses.

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THE ROLE OF HYBRIDIZATION AND INTROGRESSION IN THE DIVERSIFICATION OF ANIMALS

Thomas E. Dowling and Carol L. Secor

More common in plants?

Introgressive hybridization was **considered to occur more frequently in plants than in animals, possibly due to greater attention paid to this problem by botanists.**

Vegetative and **asexual reproduction** found in many plants provides for longer life and increased spreading capacity of individuals (or clones), whereas sexual reproduction maintains evolutionary plasticity. In addition, the **greater complexity of tissues and organ systems in animals** may require that the adaptive value of genotypes depends upon integration of a larger constellation of genes than for plants (with their simplified tissues and open systems of growth). These features would constrain the number of adaptive recombinants in animals.

Allopolyploidy (elevation of chromosome numbers due to hybridization of two or more species) is more common in plants.

Plants are also often capable of degrees of **selfing**. Many animals are obligate outcrossers, with polyploid progeny of hybridization events typically tetraploid. Such hybrids would most likely mate with diploids, producing sterile triploids. Therefore, polyploidy would be most likely found in groups exhibiting hermaphroditic or all-female modes of reproduction.

It has been argued that **faster rates of mammalian developmental change and regulatory gene evolution** cause a more rapid accumulation of hybrid incompatibilities

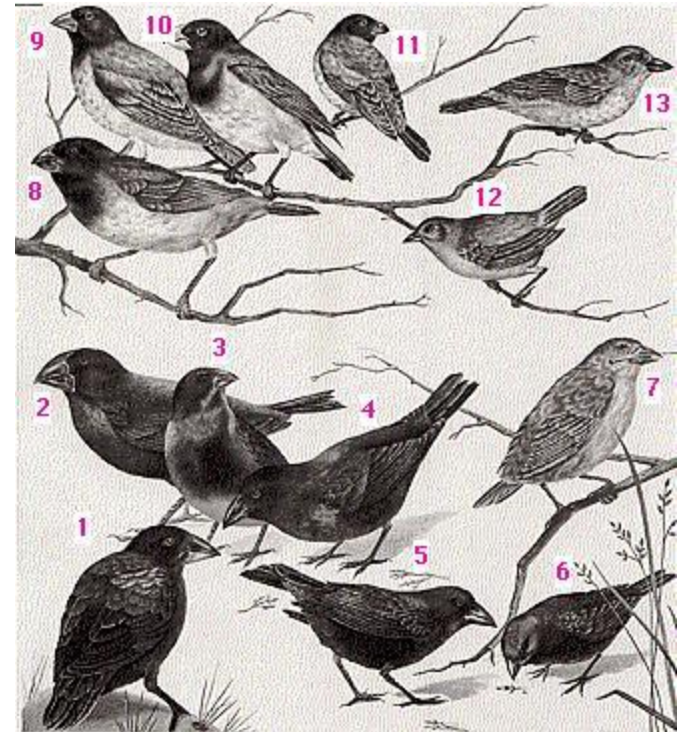
Polyploid: having more than two chromosome sets, as tetraploid (four), hexaploid (six) and so on.

Allopolyploid: having more than two chromosome sets as a result of the duplication of the number of chromosomes in a hybrid lineage following its origin by interspecific hybridization.

Introgressive role of hybridization

While not hypothesized to be hybrid taxa, **Darwin's finches** provide a strong example of the significance of **introgressive hybridization** for evolution and diversification... Because climatic stochasticity in the Galapagos Islands causes large population fluctuations in these finches, Grant & Grant hypothesized that hybridization could introduce genetic variation and **reduce inbreeding depression** during periods of small population size. Fitness of hybrids likely fluctuates with normal variation in climatic conditions, resulting in a long-term balance between hybridization and selection. Introduction of new variation by hybridization may allow selection to shift finch populations among adaptive peaks

Introgressive hybridization among taxa will quickly increase levels of variation, allowing for **rapid response to environmental change**. The potential impact of gene exchange, however, will be limited by levels of premating reproductive isolation and reduction in fitness of recombinants relative to progeny of homospecific matings. The balance of these factors will provide a subset of circumstances under which introgressive hybridization will be important



Shifts in thinking in ecology and evolution

Organisms have a tendency to track specific favorable environments, fragmenting distributions. Because of this behavior, hybridization is often found in tracts of **intermediate habitat** or where conditions favoring two taxa are found in proximity. Since such conditions tend to be patchily distributed, hybridization is often better represented as a mosaic of potentially distinctive interactions among taxa. In addition, **environments are not stable**, with resulting changes in selection pressures causing temporal shifts in the genetic composition of populations. **Environmental heterogeneity and temporal instability are conducive to formation of hybrid taxa**, especially where patches of hybrids have become isolated from both parental species.

Several groups of fishes from the western United States exhibit evidence of past introgression. Ecosystems of this region have gone through dramatic environmental change, including considerable **tectonic activity and progressive aridification**. These changes had a severe impact on aquatic ecosystems, **likely producing cycles of isolation and sympatry**. Divergent, isolated forms would have been forced together by desertification, allowing for gene exchange. Later periods of isolation would allow for stabilization and independent evolution of hybrid derivatives, resulting in taxonomic diversification.

Red wolf (*Canis rufus*) has been hypothesized to have originated through hybridization between grey wolf and coyote, stimulated by human agricultural activity. However, available data are equally consistent with an earlier origin, possibly due to **habitat changes associated with the Pleistocene glaciation**.

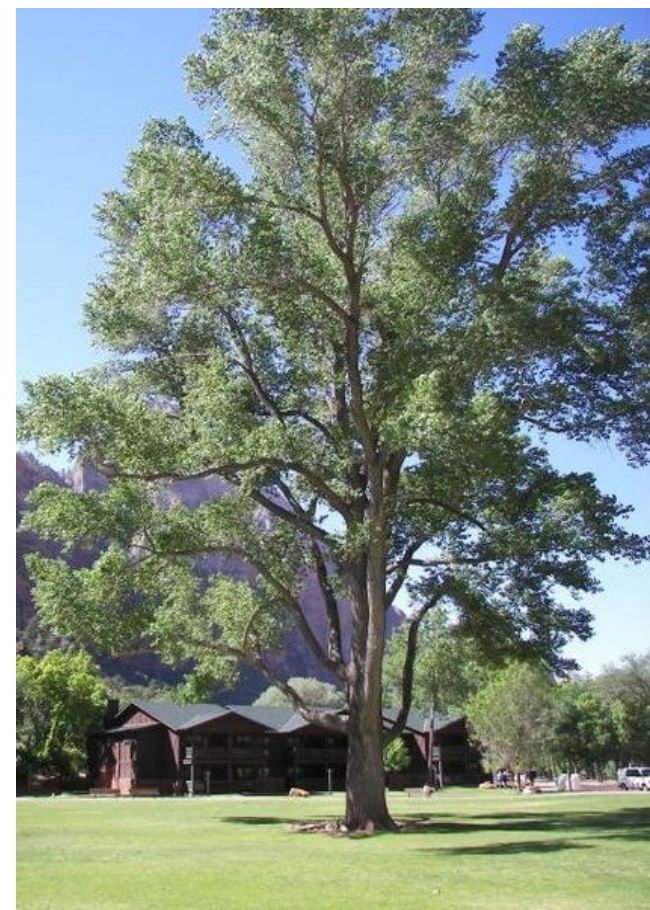
introgressive hybridization at any locality might occur anywhere along a **continuous distribution of possibilities**, ranging from introgression at one locus to... blocks of genes

levels of variation would be greatly increased, and **selection would be able to act upon segregating blocks of genic material derived from different adaptive systems instead of one or two new alleles generated by mutation.** This set of circumstances would be particularly advantageous where new ecological niches are created by changing environments, **allowing evolution to proceed at “maximum rate.”**

HYBRID POPULATIONS SELECTIVELY FILTER GENE INTROGRESSION BETWEEN SPECIES

GREGORY D. MARTINSEN,¹ THOMAS G. WHITHAM,¹ RICHARD J. TUREK,² AND PAUL KEIM¹

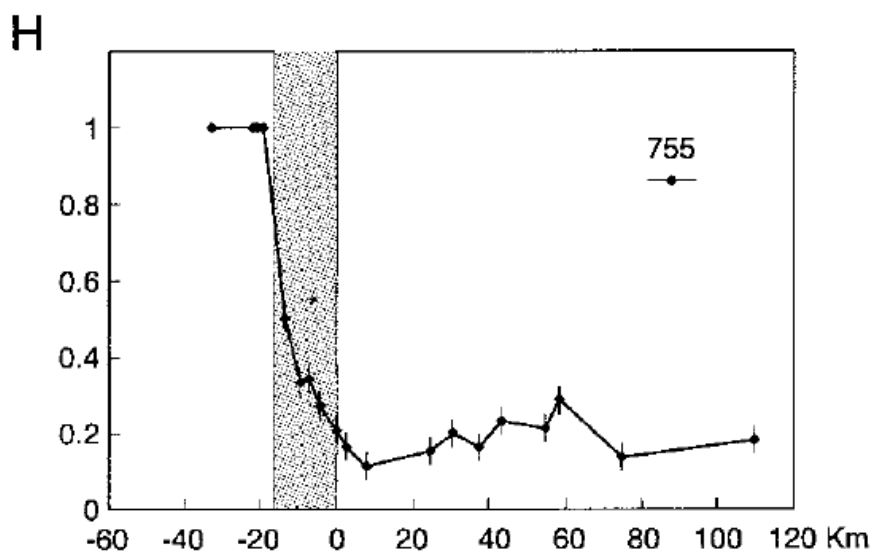
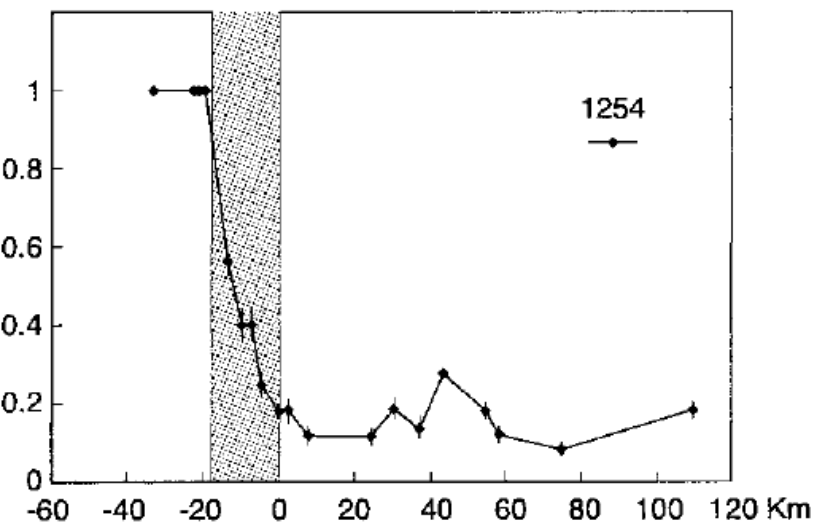
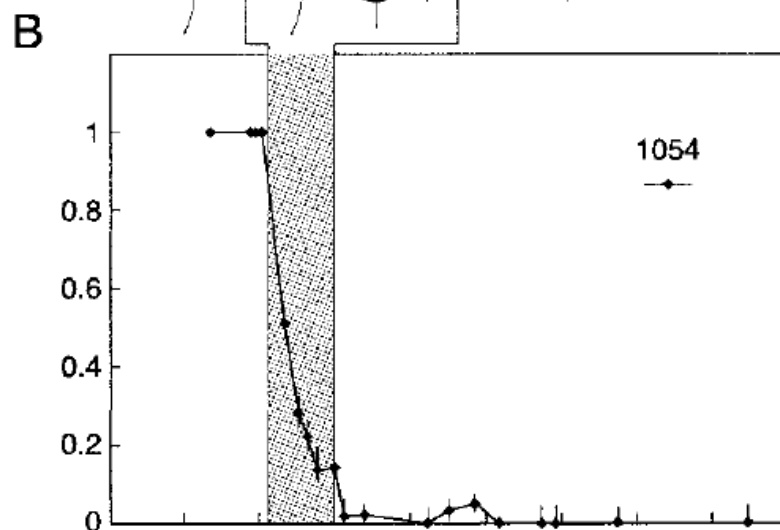
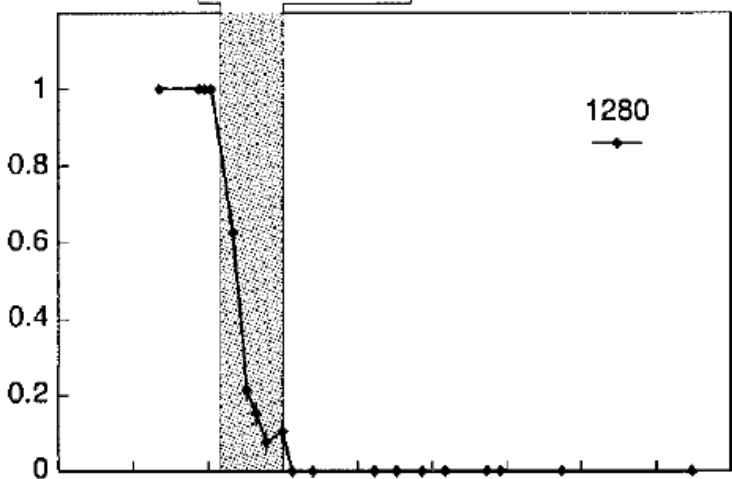
two species of cottonwoods (*Populus fremontii* X *P. angustifolia*) and their hybrids (550 trees)... we showed that **the majority of the genome is prohibited from introgressing** from one species into the other. However, **this barrier was not absolute**; Fremont cpDNA and mtDNA were found throughout the geographic range of narrowleaf cottonwood, and 20% of the nuclear markers of Fremont cottonwood introgressed



DNA fragments that introgress through several generations of backcrossing will be small, because **small fragments** are less likely to contain deleterious genes...for those markers exhibiting dispersed introgression, there is significant **variation in how far different markers introgress**, further suggesting the existence of a selective filter.

Because large segments are more likely to carry such negative genes, we predict that backcrosses carrying large segments would be selected against. Consistent with this hypothesis, selective filtering of the genome appears to be most intense in the very earliest backcross generations. Even if there are many positive acting genes in a segment, a single negative or lethal acting gene will determine the fate of all the linked genes. Thus, **a few well dispersed, negative acting genes could prohibit the majority of the genome from introgressing**. Given that nearly **80% of the markers in this study displayed only localized introgression**, negatively acting genes must be common.

Cytonuclear drag could still account for rapid nuclear marker introgression. If there are important genetic interactions between the cytoplasmic and nuclear genomes, selection for these interactions will dictate that some nuclear genomic segments introgress at comparable rates. Rapid, neutral introgression of cytoplasmic genomes would thus result in rapid introgression of particular nuclear regions.



the existence and long-term persistence of hybrid zones.

hybrid cottonwoods have been recorded in the fossil record during the past 12 million years... direct fossil evidence of ancient, persistent hybrid zones.

Hybrid zones may act as filters that **prevent the introgression of negative genetic effects, while allowing positive introgression.**

natural hybrids are common among many of the most successful and dominant taxa of the world (e.g., oaks, pines, eucalypts), suggesting that hybridization may have played an important role in their evolutionary success

COTTONWOOD HYBRIDS GAIN FITNESS TRAITS OF BOTH PARENTS: A MECHANISM FOR THEIR LONG-TERM PERSISTENCE?¹

JENNIFER A. SCHWEITZER,² GREGORY D. MARTINSEN, AND
THOMAS G. WHITHAM

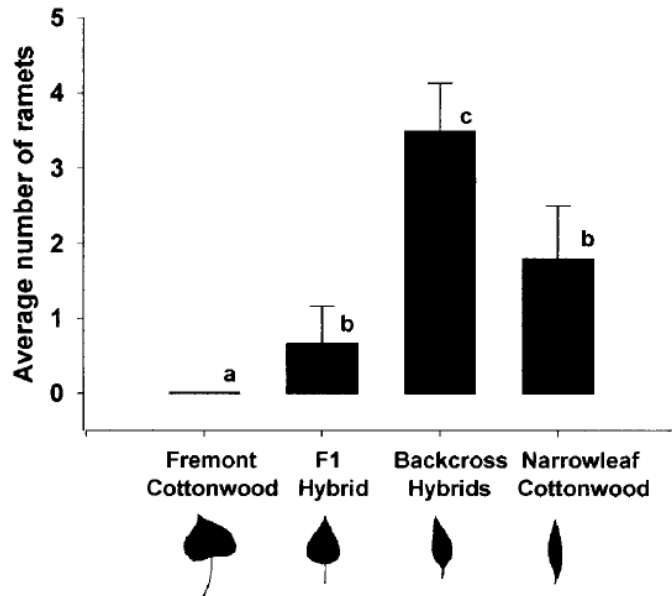


Fig. 5. Mean number of ramets produced by each *Populus* species or crosstype. In a common garden, backcross hybrids produce the most ramets ($F_{3,92} = 16.515$, $P < 0.0001$). Backcrosses genotypes produce four times as many ramets as Fremont and two times as many as narrowleaf cottonwood. Error bars represent 1 SE of the mean.

Viable hybrid seeds were produced in equal numbers to at least one of the parents and germinated at equal rates to both parent taxa, which does not indicate inherent sterility or inferiority.... surviving hybrids performed (in terms of growth) equally well or better than the parents

the high production of **asexual ramets** by hybrid genotypes may extend the lifetime of the genet and increases the likelihood that hybrid genets will reproduce sexually.

The low survival rates of seedlings from all tree types and the high survival rate of ramets indicated that this mode of reproduction could be very important to the overall fitness of hybrid cottonwoods... **under certain circumstances some hybrid crosstypes may survive as well as the parent species.**

cloning in backcross genotypes appears to be a **transgressive characteristic** as hybrids produce nearly two times more ramets than narrowleaf cottonwood. (individuals whose phenotypes exceed the parental phenotypes.)

best backcross genotype... A small portion of hybrids are much better than the average of the backcross genotypes (a fivefold difference). These patterns indicate the range of **variability of reproductive traits within hybrid genotypes is extensive** and support the idea that some hybrid genotypes (within any hybrid class) can be highly fit and have the potential to contribute to the maintenance and long-term persistence of the hybrid zone

Summary of Dowling and Secor

Extensive introgressive hybridization is often **associated with habitats disturbed** by anthropogenic activity. **More dramatic environmental changes occurred prior to human influence** that would also have been conducive to introgressive hybridization as indicated by evidence for extensive introgression in the evolution of several groups of western fishes

Changing attitudes toward hybrids and technological advances should allow for careful consideration of hypothesized hybrid taxa and will **undoubtedly increase the number of known animal hybrid taxa.**

Introgressive hybridization can influence evolution in several ways: it can cause fusion of species, genetic swamping of one species by another, elicit reinforcement of reproductive isolation between incompletely isolated species... transfer of genetic material between species, potentially facilitating their adaptive evolution, and the origin of new species. However, it can also **remain without an obvious impact if recombinant genotypes are retained in a narrow contact zone** between two species by a balance between dispersal into the contact zone and selection against hybrids

most commonly observed in zones of geographical contact between otherwise allopatric taxa... attempts to explain hybrid zones can be roughly classified as of two models.

- The **tension zone model** explains hybrid zones entirely by a balance between dispersal into the zone and selection against hybrids
- The **bounded hybrid superiority model** implicates elevated hybrid fitness in those sections of the environment where the hybrid zone lies

Many clinal hybrid zones are well explained by the tension zone model, but in others, environment- dependent hybrid superiority has been demonstrated. In such cases, hybrid zones often represent a **mosaic** of genotype distribution in space (mosaic hybrid zones), tracking patchy environments, rather than the clinal pattern



Review

TRENDS in Ecology and Evolution Vol.19 No.4 April 2004

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Hybridization and adaptive radiation

Ole Seehausen



Adaptive radiation is the rapid diversification of an ancestral population into several ecologically different species, associated with adaptive morphological or physiological divergence. Although often occurring within combined geographical regions (e.g. large lakes or island archipelagos), much of the functional diversity of life might have arisen during episodes of adaptive radiation. Relatively broad agreement exists on several factors that might facilitate adaptive radiation, although these have proven difficult to quantify. They include release from competition in an underutilized environment (e.g. a new lake), key evolutionary innovations that enable utilization of resources that were there but could not be utilized previously (e.g. echolocation in bats) and mating systems that are conducive to rapid divergence. However, variation in **these criteria is, in many cases, insufficient to explain the adaptive radiation** of some and the absence of radiation of other taxa that share the same characteristics and find themselves in the same environmental circumstances. For example, Lake Victoria in East Africa was colonized by five unrelated lineages of cichlid fish at the same time, but whereas one radiated into (500 new species, the other four did not diversify.

Theory of hybridization and adaptive radiation

If a population that contains sufficient variation at functional loci arrives in an adaptive landscape that comprises **multiple underutilized fitness peaks** ('niches'), and if only subsets of **these peaks can be effectively utilized by any one functional genotype**, several populations of functional genotypes might emerge rapidly by multiple events of ecological speciation. By instantaneously elevating heritable variation in ecologically relevant traits **in situations where the potential for ecological diversification is unusually high, hybridization upon invasion of new environment should therefore facilitate rapid adaptive radiation**

as exemplified by waterfleas of the *Daphnia longipes* complex in northwest European lakes. In a multimodal fitness landscape, where fitness peaks are seasonal niches mediated by changing abundances of predators of, and prey for *Daphnia*, different fitness peaks are occupied by parent species and hybrid taxa.

After a radiation has progressed to a stage with two or more incipient species, **occasional or localized hybridization between these species would facilitate further ecological diversification**... the rapid generation, by hybridization, of new adaptive trait combinations, which are suitable for utilizing resources that were not utilized previously

Hence, **hybridization would maintain and prolong the adaptive radiation momentum**. Such a mechanism has recently been suggested to explain the rapid evolution of mimicry rings in *Heliconius* butterflies.

What next...

As the number of species increases and unexploited resources become scarce, selection as experienced by individual populations would change from directional or disruptive to stabilizing. **The probability that recombinant hybrid genotypes find underutilized niches in which they enjoy equal or higher fitness than do their parents would diminish**... depression of ecological fitness of hybrids relative to that of parental types would tend to reinforce premating isolation... the frequency of interspecific hybridization would decrease and fewer hybrid genotype populations would become established as new species, whilst genomic incompatibilities would begin to accumulate between existing species.

However, **radiations might never reach this stage if the environmental conditions are unstable or if successively evolved innovations open up new niche dimensions**, allowing for successive rounds of radiation



Review

TRENDS in Ecology and Evolution Vol.20 No.5 May 2005

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SCIENCE

Hybridization as an invasion of the genome

James Mallet



ELSEVIER

Biological Conservation 89 (1999) 143–152

BIOLOGICAL
CONSERVATION

Rapid displacement of native species by invasive species: effects of hybridization

Gary R. Huxel*



Review

TRENDS in Ecology and Evolution Vol.20 No.5 May 2005

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SCIENCE

Genes invading new populations: a risk assessment perspective

Rosie S. Hails and Kate Morley

It has been suggested that **interbreeding increases the threat of extinction for a number of species due to hybridization introgression...**

In cases where related taxa are able to interbreed, introductions may lead to the introduced taxa dying out, coexistence, new hybrid taxa or extinction of the native taxa.

Historically, geographical isolation has been a major factor in limiting the impacts of hybridization and introgression. Today, however, taxa are being brought into contact with related taxa from which they have been isolated through many anthropogenic pathways

- the movement of ballast water
- introduction of nurse stocks of plants
- incidental movement of herbivores and parasitoids

Human-mediated **introductions can be frequent and re-occurring**, greatly increasing immigration rates

Given the number of cryptic species and the high rates of human-mediated species introductions, **extinctions may be on the increase from the effects of hybridization** alone.

How does modern hybridization differ from historical (pre-human)?

- Higher introduction rates
 - Allopatric taxa brought together
 - Hybridization of habitat
-
- especially important because the taxa that are most threatened by introgression and hybridization have low population sizes and restricted ranges.
 - potential loss of **genetic integrity of native populations** through selective stocking of non-native individuals
 - species that are most at risk to hybridization are ones that have external fertilization (e.g. as broadcast spawning marine invertebrates and outcrossing plants- wind pollinated taxa)

Difficulties in detecting hybridization:

- Sympatric hybridization has often been studied using mitochondrial sequence data, although, on its own, mtDNA provides very little information about hybridization.
- gene flow is hard to separate from ancestral polymorphism
- Introgression can be highly selective, affecting only some parts of the genome, whereas other genomic regions strongly affected by divergent selection remain virtually isolated

The Case for Genetic Engineering of Native and Landscape Trees against Introduced Pests and Diseases

Abstract: *Many important native forest trees and familiar landscape trees of the northern temperate zone have been devastated by introduced pests and diseases. Without human intervention, many of these trees will become extinct or endangered. As trade and travel increase, it is likely that further devastating epidemics will occur. To undo the damage that has been done, we suggest limited, cautious transfer of resistance genes from the original host species in the source region of the pest or disease. The transgenic trees can then be replanted in forests or countryside to resume their original ecological niche. This method could have some advantages over tree-breeding techniques, including introgression. For instance, fewer tree generations would be required and fewer unnecessary genes of the non-native tree species would be introduced. Furthermore, once the technique is perfected it would be possible to separately add resistance genes to local land races of trees, for reintroduction to their original habitats, without relying on intensive and lengthy local introgression programs. Practical problems with identifying and transferring resistance genes do exist, however, and somaclonal errors might lead to genetically engineered trees that do not resemble their parent in growth form. Nevertheless, we believe that, with further work, this approach may offer a preferable alternative to introgression with non-native trees.*

American chestnut- a use of hybridization



INTRODUCTION HISTORY AND HABITAT VARIATION EXPLAIN THE LANDSCAPE GENETICS OF HYBRID TIGER SALAMANDERS

BENJAMIN M. FITZPATRICK^{1,3} AND H. BRADLEY SHAFFER²

Current question: **What factors influence the spatial, temporal and genomic spread of genes** from one species to another?

- Environmental selection
- Hybrid vigor/ outbreeding depression
- Reproductive incompatibilities
- Dispersal
- Abundance

Hybridization is likely to become more common in coming decades as species' distributions shift



Molecular Ecology (2009) 18, 2228–2242

doi: 10.1111/j.1365-294X.2009.04137.x

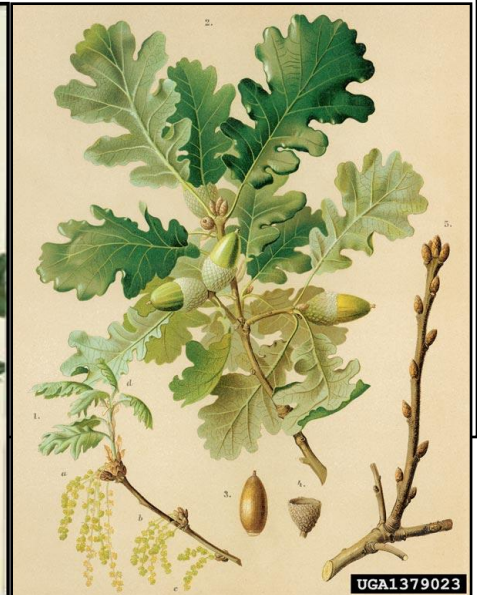
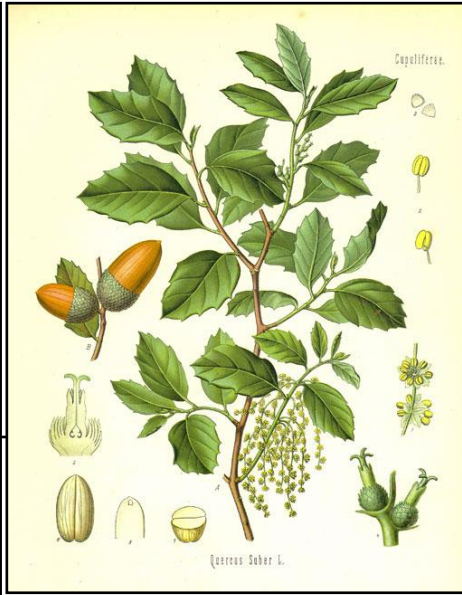
Species relative abundance and direction of introgression in oaks

O. LEPAIS,*†‡ R. J. PETIT,*† E. GUICHOUX,*† J. E. LAVABRE,*†§ F. ALBERTO,*†
A. KREMER*† and S. GERBER*†

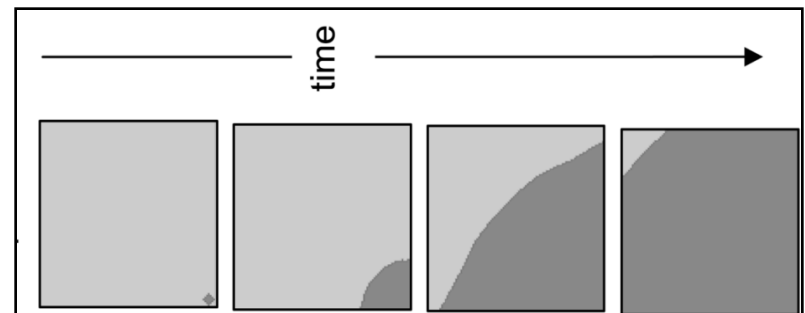
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Oaks- Quercus

- A classic “species problem”
- Number of “species” of oaks in Europe ~25, *petraea* and *robur* are most common... Ecological specialization (soil, succession), local abundance



- General idea
 - **less abundant species is “swamped”**
- One current model
 - Currat et al. 2008
 - introgression from the local to the invader
 - gene propagation with growth
- Empirical evidence
 - backcrosses often being towards the more abundant (Eucalyptus, Juglans)



- **hybridisation is not rare and it is a contemporary process**
- we found a deficit of hybrids involving locally dominant species whereas **less frequent species tend to be over-represented among hybrids**
 - species that came more recently in contact, for which **reinforcement** would not have developed
 - rare species could be over-represented among hybrids because of **their difficulty to mate with other rare conspecific partners**.... should receive abundant heterospecific pollen, which would increase hybridisation

Our results indicate that (hybridization) should not be viewed as a fixed parameter but as a variable one that depends on factors such as the local composition

- **“hybrids involving a species not identified during field work... remarkable in the well characterised stand where only pedunculate and sessile oaks had been described”**
 - Two hypotheses can explain such observations: hybridisation by long-distance pollen dispersal or past local extinction of one species
- bias in data, a challenge
 - “some hybrid oaks could be characterised by an intermediate leaf morphology and intentionally (or not) avoided during sampling”

Massive deforestation during the last 3000 years by human exploitation and land clearing for agriculture... difficult to estimate original species distribution and the possibility of local extinction

Human impacted landscapes facilitate hybridization between a native and an introduced tree species



Human impacted landscapes

Intersection of human and natural landscapes
(fragmentation, disturbance, pathogens)

Population demography, mating patterns, dispersal,
reproductive success, resources, species...

Population viability, conservation

Why forests?

Ecological importance: mast, habitat, food, fuel, carbon storage, ecosystem stability and function

Evolutionary interest: non- model reproductive characteristics- long life span, overlapping generations, massive and highly uneven reproductive output, long distance dispersal¹

¹ Petit and Hampe 2006, Petit *et al* 2008

Human impacted landscapes- hybridization

Influence of anthropogenic landscapes on spatial and temporal dynamics of gene flow between species ²

Questions:

1. What is the extent of hybridization? Is it influenced by the landscape?
2. Are advanced generation hybrids produced? Are the types of hybrids produced influenced by the landscape?
3. What is the direction of gene flow? Is it influenced by the landscape?

To predict the outcome of introductions, and of conservation actions ¹

¹Allendorf *et al.* 2001, Wolf *et al.* 2001, Levin 2002

²Wiegand 1935, Fitzpatrick & Shaffer 2004

Study system- Butternut, *Juglans cinerea*

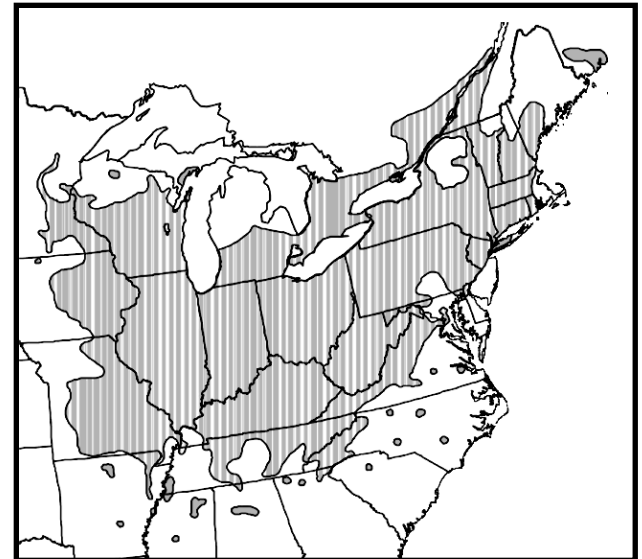
Model for early successional species¹

- Lives to ~ 60-70 years
- Reproductive at ~10-15 years
- Typically a riparian species

Currently threatened, protected

- Introduced pathogen
- Habitat loss
- Habitat quality
- Hybridization²

Japanese walnut (*J. ailantifolia*)
introduced in late 1800s, widely planted



¹ *Salix, Platanus, Populus, Liriodendron, Betula*

² Ostry & Woeste 2004, Hoban *et al.* 2009, Anagnostakis 2009





1. Rates of hybridization increase with human impact

- Open conditions accelerate the temporal dynamics (pollen flow, higher reproductive success)
- Higher rates of introduction
- Selective advantage for hybrid offspring

2. Hybrid categories differ by habitat

- **Advanced generation hybrids more likely with human impact**

3. *J. aillantifolia* are more likely to be the **seed parent of hybrids**

- Frequent observation in other systems
 - a) Relative abundance
 - b) Partial one way incompatibility

Conclusions

Summary of findings:

Bidirectional, advanced generation hybridization over a large geographic area, but **large variance between sites**

Agrees with recent studies in trees¹ on the role of abundance and/ or human activity

How does this study contribute to population/ conservation genetics?

Argues for the influence of habitat on mechanisms other than selective advantage; possibility of difference dynamics occur in short and long lived species

Fragmentation itself does not contribute to high rates of hybridization

¹Thompson *et al.* 2010; Burgess *et al.* 2005; Zalapa *et al.* 2007

²Martin *et al.* 2006; Rieseberg *et al.* 2003; Hamzeh *et al.* 2007; Metcalf *et al.* 2008; Fitzpatrick, Shaffer 2007; Currat *et al.* 2009

Conservation management

Notes and recommendations:

- Hybridization predominantly occurs in a specific habitat- anthropogenic landscapes
- High proportion of F_1 hybrids suggests hybridization is ongoing
- Few *J.a.* individuals were observed

1. Hybridization is likely to remain limited in the near future, but rare hybridization events can occur anywhere; continued monitoring is recommended
2. Hybridization can continue long after eradication/ halting introduction
3. Low level of hybridization is likely in other tree species¹; further investigations are needed, especially in trees introduced in larger numbers
4. Native habitat seems to serve as partial barrier to hybridization, by limiting either introduction rates or dispersal; even small fragments seem effective

These are important considerations, for either the utility or danger of hybrids

¹ Burgess et al 2005, 2008

Summary of topics

1. Hybridization, introgression, hybrid speciation
2. Hybridization of habitat (natural and man made)
3. Early questions about hybridization
4. Genetics of hybrids (epistasis, number of genes, transgressive segregation)
5. Importance of rare events in evolution
6. Hybrid zones
7. Hybridization and adaptive radiation
8. Hybrids and conservation of rare species
9. Hybrids and abundance, landscape, introductions