

## Review



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## Evolutionary biology

# Adaptive introgression: a plant perspective

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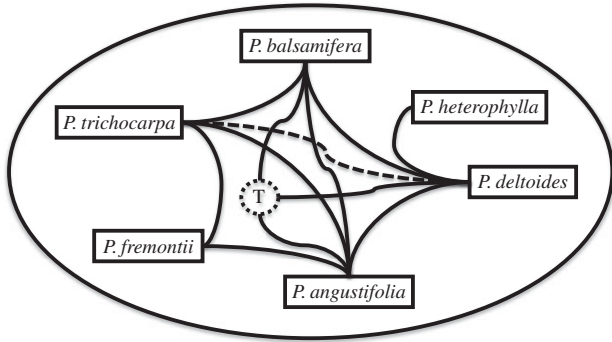
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Introgression is emerging as an important source of novel genetic variation, alongside standing variation and mutation. It is adaptive when such introgressed alleles are maintained by natural selection. Recently, there has been an explosion in the number of studies on adaptive introgression. In this review, we take a plant perspective centred on four lines of evidence: (i) introgression, (ii) selection, (iii) phenotype and (iv) fitness. While advances in genomics have contributed to our understanding of introgression and porous species boundaries (task 1), and the detection of signatures of selection in introgression (task 2), the investigation of adaptive introgression critically requires links to phenotypic variation and fitness (tasks 3 and 4). We also discuss the conservation implications of adaptive introgression in the face of climate change. Adaptive introgression is particularly important in rapidly changing environments, when standing genetic variation and mutation alone may only offer limited potential for adaptation. We conclude that clarifying the magnitude and fitness effects of introgression with improved statistical techniques, coupled with phenotypic evidence, has great potential for conservation and management efforts.

## 1. Role of plants in the study of adaptive hybridization

In the early twentieth century the botanist J.P. Lottys vigorously championed the role of hybridization in evolution [1]. Although Lottys's views now seem primitive in the light of modern genetics, he undoubtedly primed a succeeding generation of botanists to look at hybridization seriously. Arguably his most enduring contribution was to coin the term 'syngameon' which he applied, for instance, to hybridizing European species of birch trees. This concept was later developed by Grant [2], who identified many plant syngameons, and this in turn influenced the development of the ecological species concept as exemplified by oaks [3]. A syngameon is a group of otherwise distinct species interconnected by limited gene exchange, i.e. the most inclusive interbreeding evolutionary unit (figure 1). The sharing of allelic diversity between a group of species in a syngameon has clear evolutionary consequences.

Another key concept to originate from plants was that of 'introgression', coined by Anderson and exemplified by his studies of hybridization in spiderworts [4]. Introgression refers to the transfer of a small amount of the genome from one parental taxon (usually species) to another by hybridization and repeated backcrossing. From the beginning, Anderson was clear about the potential adaptive effects of introgression: 'the final result will depend upon the balance between the deleterious effects of the foreign germplasm and its advantageous effects in the areas where the hybridization has taken place or to which the hybrids may spread' [4, p. 396]. Since Anderson, the evolutionary consequences of syngameons and introgression have been enormously developed and extended both in plant systems [5–8] and more widely [9].



**Figure 1.** Syngameon of North American poplars (*Populus*). Lines represent hybrid zones connecting the largely parapatric species. 'T' indicates the three-species hybrid zone in southern Alberta. *P. trichocarpa* × *P. deltoides*, although common in cultivation, is rare in the wild (indicated with dotted line). Adaptive introgression has been demonstrated between *P. trichocarpa* and *P. balsamifera* (see text) but potentially occurs more widely across the syngameon.

This review focuses specifically on 'adaptive introgression', defined here as the transfer by introgression of relatively small genomic regions from a donor species that have positive fitness consequences in the recipient species. We discuss the key role that plants have had, and will have, in the development of the field, and outline the methodology required to demonstrate adaptive introgression, in both plant and animal systems, including requirements for the future.

## 2. Adaptive introgression

According to current views of divergence along the speciation continuum [10], species boundaries are characterized as being 'porous' or 'semipermeable', with the latter at least implying that differential introgression results from a selective process [11]. Although much of this recent work has been conducted in animals, there has also been considerable contribution from plant systems [12–14] and a plant perspective is particularly important owing to the frequency of plant hybridization. It is estimated that around 25% of plant species exchange genes with relatives, almost double the rate suggested for animals [15].

Although stochastic processes could predominate during introgressive hybridization in nature, adaptive introgression occurs when introgressed alleles are maintained by natural selection [16–18]. Adaptive introgression has now emerged as an important source of variation available for evolution, alongside de novo mutation and standing variation, widening the pool of genetic variation available for adaptation [19]. Furthermore, introgressed alleles may result in epistatically favourable gene combinations within the new genomic background and further accelerate adaptation [20].

Loci associated with broadly advantageous traits are expected to introgress more frequently [21–23], while alleles that contribute to reproductive isolation will introgress little or not at all [20,24,25]. Local adaptation can, therefore, potentially contribute to both reproductive isolation and its breakdown, depending on whether locally adapted alleles contribute to genetic incompatibilities, for instance as locally adaptive alleles may be specific to a genomic background and cause outbreeding depression in alternative backgrounds [26,27]. Where not, introgressed variation may readily facilitate local adaptation in the recipient species from the already

adapted donor species [15,21], and this is the process we are primarily concerned with here.

## 3. Methods to detect adaptive introgression

The detection of introgression is generally straightforward, but showing that introgression is adaptive ideally requires multiple lines of evidence to demonstrate beyond reasonable doubt that the introgressed genomic regions from a donor species have a fitness effect in the receiving genomic background (tables 1 and 2). The evidence necessary to document adaptive introgression includes the following main steps:

- (1) Introgression—identifying true introgressed regions by distinguishing recent transfer from shared ancestral genetic variation [65,28]. A rapidly growing toolbox (table 1) facilitates tests for introgression of genomic blocks relative to alternative scenarios, such as incomplete lineage sorting [26,28,31,32,39]. Many of these approaches exploit the fact that introgressed blocks are generally longer than segments originated from incomplete lineage sorting and that the expected length of introgressed regions depends on the time since admixture [30,67].
- (2) Genomic signature of selection—uncovering the genomic signature of selection, for instance by demonstrating significantly greater persistence and spread of introgressed regions than expected by chance [33,38]. The environmental context in which hybridization occurs, together with dispersion distance and natural selection are key factors underlying the geographical patterns and spatial scale of introgression [66,68,69].
- (3) Adaptively relevant phenotypic variation—demonstrating that introgressed alleles have adaptively relevant phenotypic consequences [18,29]. A particularly promising approach that has been enabled by genome data is admixture mapping. Almost a decade ago, a review [39] discussed potential applications of admixture mapping in the plant genus *Helianthus* [64], in two European *Populus* species, *Populus alba* and *Populus tremula* [70], and the lake whitefish (*Coregonus* spp.) species complex [51]. This review noted other hybridizing taxa that showed promise for admixture mapping, including hybrid populations of *Antirrhinum* and of *Silene*, *Peromyscus* mice species, invasive and native sculpins, *Heliconius* butterflies and sticklebacks [39]. Recently, for instance, local ancestry and admixture mapping has been used in sticklebacks (*Gasterosteus aculeatus*) to identify genomic regions associated with divergence in male nuptial colour [52], in *Mimulus* to determine the genetic basis of trichome differentiation between *Mimulus guttatus* adapted to geothermally heated soils and nonthermal putative ancestors [63], and in two North American *Populus* species (*Populus trichocarpa* and *Populus balsamifera*) to explore if introgressed regions are driving variation in adaptive traits and contributing to the northern range expansion of *P. trichocarpa* [61,62] (table 2).
- (4) Fitness—direct measurement of a fitness effect of the introgressed region, and its resultant phenotype, in the receiving species [22,71]. This is the most critical step, yet often inadequately addressed. A strong demonstration of adaptive introgression ideally involves experimentally assaying the

**Table 1.** A summary of the different classes of investigation used in studies of adaptive introgression.

class of investigation	examples	notes
I. <i>introgression</i> (genome-wide-based methods to infer introgressed blocks)	Patterson's <i>D</i> statistic, <i>fd</i>	the Patterson's <i>D</i> statistic detects an excess of shared derived alleles between species but does not distinguish introgression from ancestral population structure or indicate which genomic regions show such an excess. <i>fd</i> , a modified version of a statistic developed to estimate the genome-wide fraction of admixture, provides an improved method of identifying candidate introgressed regions [28]. The joint distribution of <i>fd</i> and mean absolute genetic divergence ( <i>dXY</i> ) statistics may be useful for differentiating introgression from shared ancestral variation at individual loci
	tract length and linkage disequilibrium (LD, <i>S*</i> statistics)	these statistics aim to capture events of introgression by incorporating information regarding tract length and linkage disequilibrium. These approaches exploit the fact that introgressed blocks are generally longer than segments originated from incomplete lineage sorting and that the expected length of introgressed regions depends on the time since introgression [30]
	probabilistic models such as hidden Markov models (HMM)	these methods have been used to reconstruct high-resolution recombination maps in admixed populations [31] and detect fragments introduced by introgression. Under this approach, initially proposed and implemented by [32], the ancestry of each genetic marker in the genome is a hidden random variable with two states (e.g. homospecific ancestry, mixed ancestry) which are estimated from the data
II. <i>genomic signature of selection</i>	detection of locally varying selection: integrated haplotype score (iHS), extended haplotype homozygosity (EHH), Tajima's <i>D</i> , Fay and Wu's <i>H</i> , and variations on <i>F<sub>ST</sub></i>	these methods are based on the haplotype structure or the distribution of allele frequencies compared with that expected under neutrality [33–35]. However, the patterns in introgressed regions (selected or not), such as increased LD, are exactly those used by many statistical analyses to test for selection. Inferences of selection cannot, therefore, rely solely on the patterns generated by introgressed segments but rather should be accompanied by additional pieces of evidence [36]
III. <i>adaptively relevant phenotypic variation</i>	quantitative trait loci (QTL) studies, genome-wide association studies (GWAS)	adaptive introgression implies that the introgressed genomic regions produce phenotypic variation that can be selected on. It is, therefore, also necessary to find associations between introgressed DNA and a phenotype known or suggested to confer a fitness advantage. Formerly this was done by QTL analysis [37] but the advent of whole-genome data has made this even more powerful, for instance using genome-wide association scanning (GWAS) approaches [35,38]
	molecular function	functional differences (such as differential expression or protein structural differences) between introgressed and non-introgressed alleles can be used to infer phenotypic effects, when the trait being controlled by an introgressed block is challenging to measure, or when there are complex interactions between genetic factors and the environment
	admixture mapping	admixture mapping is a powerful statistical approach to map genes associated with phenotypic traits in hybridizing or introgressed populations [39,40]. Correlating local ancestry with a particular phenotype requires genotype data from both the admixed and parental reference populations to quantify excess admixture as well as trait information from, at least, the admixed individuals. This method has been used extensively to map genes associated with diseases or traits with differential risk by ancestry in human populations [40]. However, the number of studies implementing this approach in non-human organisms, including plant species, is substantially lower

(Continued.)

Table 1. (Continued.)

class of investigation	examples	notes
IV. fitness	common garden and reciprocal transplant experiments	such experiments are best set up in a reciprocal manner [41], although experimental designs involving single environments (e.g. hybrid or parental habitats) can also be informative, as long as the tested biological material represents the whole breadth of genotypes relevant to the questions under study [42]. Common garden and transplant experiments involving hybrids (or crosses between highly divergent populations) have repeatedly uncovered important fitness effects of single traits or quantitative trait loci (QTL) in the wild [21,42–44]
	polygenic modelling	a promising approach to link studies of phenotypes and fitness in an adaptive introgression context involves polygenic modelling via sparse whole-genome regression methods [45]. This family of methods potentially allows disentangling the effects of direct and indirect selection on individual loci from genome-wide marker data [46], analogous to very widely used methods of measuring selection on correlated characters [47]

Table 2. Representative studies on adaptive introgression including examples in birds, fish, insects, mammals and plants. For each example, we note the type of evidence used, including tests for (1) introgression, (2) genomic signature of selection, (3) adaptively relevant phenotype and (4) direct fitness measurements.

species group	organism	natural hybrids	(1) introgression	(2) selection	(3) phenotype	(4) fitness	references
bird	flycatcher ( <i>Zimmerius</i> )	yes	yes	no	yes	no	[48]
fish	trout ( <i>Onchorhynchus</i> )	yes	yes	no	no	no	[49]
fish	cichlid fishes ( <i>Astatotilapia</i> )	yes <sup>a</sup>	yes	no	yes	no	[50]
fish	lake whitefish ( <i>Coregonus</i> )	yes	yes	yes	yes	no	[51]
fish	stickleback ( <i>Gasterosteus</i> )	yes	yes	yes	yes	no	[52]
insect	butterflies ( <i>Heliconius</i> )	yes	yes	yes	yes	no	[23]
insect	malaria mosquitoes ( <i>Anopheles</i> )	yes	yes	yes	yes	yes	[53]
mammal	<i>Canis</i> (wolf and coyote)	yes	yes	no	yes	no	[54]
mammal	pigs ( <i>Sus</i> )	no	yes	yes	yes	no	[55]
mammal	house mice ( <i>Mus</i> )	yes	yes	yes	yes	yes	[56]
mammal	humans ( <i>Homo</i> )	yes	yes	yes	yes	yes	[57]
plant	<i>Arabidopsis</i>	yes	yes	yes	yes	no	[58]
plant	spruce ( <i>Picea</i> )	yes	yes	yes	yes	no	[59]
plant	oak ( <i>Quercus</i> )	yes	yes	yes	no	no	[60]
plant	poplar ( <i>Populus</i> )	yes	yes	yes	yes	no	[61]
plant	poplar ( <i>Populus</i> )	yes	yes	yes	yes	no	[62]
plant	monkeyflower ( <i>Mimulus</i> )	yes	yes	yes	yes	no	[63]
plant	sunflower ( <i>Helianthus</i> )	no	yes	no	yes	yes	[21,64]
plant	<i>Iris</i>	no	yes	no	yes	yes	[29]

<sup>a</sup>Human-mediated introgressive hybridization.

fitness effects of heterospecific allele combinations [72,73]. Plants are promising organisms for this as common garden trials can be readily established. These may easily be replicated in the case of clonally propagated plants. More experiments of this type would be highly desirable for validating putative cases of adaptive introgression, especially in study systems in which whole-genome sequencing of many individuals from admixed populations is feasible.

The dramatic increase in the amount of genomic data has allowed the rapid accumulation of evidence for introgression (step 1) as well as candidate genomic regions for adaptive introgression (step 2) but information on the genetic architecture of introgressed phenotypic traits (step 3) lags behind. Step 4 (direct measurement of fitness) has benefited least from genomics, and more work in this area is urgently required.

## 4. Adaptive introgression in plants: some recent examples

The phrase 'adaptive introgression' first appears in the Web of Science database in the year 2000, in a study of hybrid *Rhododendron* in the British Isles [74]. Since then (up to end of 2017) 163 papers have mentioned the phrase in key words, abstract or title, and 125 of these have appeared since the latest major review on adaptive introgression, which focused largely on animals [22]. The large increase of studies in this field has been strongly influenced by the increased availability of genomic information for an expanding range of species, which has very often revealed the importance of gene flow during or after speciation.

Introgression of adaptive genetic variation has now been well documented in a number of plant species, such as *Senecio* [75] and *Helianthus* [21,64,76]. For example, *Helianthus annuus* ssp. *texanus* (a hybrid of *Helianthus debilis* and *H. annuus*) gained increased herbivore resistance from its *H. debilis* parent, suggesting that introgression of biotic resistance traits was important in the adaptation of this hybrid subspecies [21].

Adaptive trait transfer has also been reported in the flood-tolerant *Iris fulva* and the dry-adapted *Iris brevicaulis* [29]. In artificial backcrosses of these two species, the ability to survive extreme flooding conditions was strongly influenced by the presence of introgressed *Iris fulva* alleles located throughout the genome [29]. In a serpentine autotetraploid, *Arabidopsis arenosa*, adaptation to drought, as well as mineral nutrient deficiency and phytotoxic levels of metals, appears to have been driven by genetic variants arising locally but also by capturing alleles from *Arabidopsis lyrata*, a diploid that independently colonized serpentine barrens [58].

In long-lived tree species, a number of studies have reported the contribution of interspecific hybridization to local adaptation. Examples include spruce [59,77], *Eucalyptus* [78], oak [79] and poplars. Poplar trees (*Populus* spp.) have emerged as models for population genomic studies of adaptation owing to porous species barriers and a wealth of genomic resources available, including sequenced genomes and annotated gene models [80,81]. Large 'mosaic' hybrid zones of *P. alba* and *P. tremula* along European river systems have been used in admixture mapping of the sort described above (in §3). Hybrids of these poplar species revealed conspicuous additive and over-dominant genetic effects [82] as well as heterozygote excess for markers tagging phytochemical defence trait QTL [83]. Barriers to introgression appear strong but nevertheless permeable between these species [84–86].

The first study documenting fine-scale genomic introgression patterns and identifying adaptive introgression at the gene level in forest trees was carried out in two sibling poplar species, ecologically divergent and adapted to strongly contrasting environments, *P. trichocarpa* and *P. balsamifera* [61,62]. This work was carried out within the context of a large-scale genomics project that included landscape genomics [34] and phenotypic [87] components as relevant background to studies of adaptive introgression.

## 5. The conservation implications of adaptive introgression

Should conservationists try to prevent or encourage gene exchange between species? This important question has

been debated widely in terms of the risks of genetic swamping and outbreeding depression on the one hand, and the expression of transgressive advantageous characters in hybrids and their potential transfer between species on the other [88]. Forests in particular are increasingly threatened by a changing climate and maintaining the health of tree populations is particularly challenging, as rapid climate change threatens to disrupt the match between local populations and climate [89]. Improving our understanding of the importance of adaptive introgression as a source of variation for genetic adaptation will allow better prediction of responses to conservation threats [90]. This is likely to become an increasingly urgent research topic in the future.

## 6. Future

While advances in genomics have contributed to our understanding of introgression and porous species boundaries (task 1) and the detection of signatures of selection in introgression (task 2), the investigation of adaptive introgression requires more than this: specifically, links to phenotype and fitness (tasks 3 and 4, as discussed above). There is currently a relative dearth of studies that directly determine the fitness consequences of genomic regions exchanged between divergent populations or species (table 2), although useful analytical tools are starting to emerge [45,46].

To better determine adaptive introgression, improved statistical techniques, coupled with more phenotypic data, could help. This type of method requires a realistic demographic scenario to distinguish introgression from other processes [91]. Once these complexities have been dealt with, phenotypic and fitness effects can readily be mapped by extending available genome-wide association study (GWAS) approaches [45,46]. The gold standard will be to determine experimentally whether introgression confers increased fitness in a relevant ecological context. Here, plants may play an important role as they are relatively amenable to experiments through common garden and reciprocal transplant approaches and ease of clonal propagation.

The widespread occurrence of natural hybridization in plants and the frequent high fertility of interspecific plant hybrids will provide a multiplicity of experimental possibilities. A 'breeding' approach, was used in *Mimulus* to transfer a flower colour allele between species and demonstrate a strong impact on pollinator visits under natural conditions [92]. Similarly, applied plant breeding provides a large number of analogous experiments: it is commonplace to transfer fitness traits from wild species into domesticated crop species by 'introgression breeding' under strong artificial selection. Resistance traits to more than seven pests have been transferred to rice from wild species [93]. By contrast, interspecific crosses are rather rarely used in animal breeding.

Lastly, it can be noted that closely related plant species vary in barriers to gene exchange, from complete cross-fertility to the major sterility barrier provided by differences in ploidy level (an easily studied sterility barrier that is extremely common in plants but rarer in animals). Remarkably, in plants at least, natural selection can introgress genes across the almost complete sterility barrier provided by ploidy [94]. This shows that even undetectable levels of gene flow are little impediment to adaptive introgression at an evolutionary time-scale and consequently adaptive introgression may be far more pervasive than we currently imagine.

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