Adaptive introgression in the context of climate adaptation

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Abstract

As the biosphere faces accelerating environmental disruption, including climate change, and the prospect of an anthropogenically-driven mass extinction, understanding the mechanisms that enable species to adapt has become increasingly urgent. One mechanism attracting growing attention is adaptive introgression, the transfer of beneficial genetic variation between closely related species. Although frequently invoked as a potential driver of adaptation to rapid environmental change, including climate change, its overall importance remains debated. In this review, we adopt a balanced, evidence-based perspective. After introducing approaches for identifying potential donor and recipient species of introgression events, we review both the classical methods for detecting introgression and selection, and the recent methodological advances that allow their joint inference. To date, we have identified roughly twenty published studies that provide at least partial support for a connection between introgression and climate-related adaptation, most often involving adaptation to climatic oscillations during the late Pleistocene rather than to contemporary climate adaptation. Although adaptive introgression is frequently invoked in evolutionary and conservation biology, we highlight a persistent gap between its theoretical expectation and the scarcity of well-documented, functionally or ecologically validated examples. Considering the pressing challenges to preserve biodiversity and improve predictions of adaptive potentials under climate change, addressing this gap is of paramount importance. We conclude by proposing key research directions of research at the intersection of macroevolution, microevolution, and the evolutionary ecology of communities.

Keywords: *climate adaptation, hybridization, gene flow, selection inferences, adaptive introgression methods, species resilience, evolutionary ecology, conservation genomics*

1. Introduction

One of the most pressing questions in evolutionary biology today is how species adapt to rapid environmental shifts, and whether such adaptive capacity will suffice to withstand the accelerating climate crisis. Adaptation is well known to be primarily driven by two mechanisms: new (*de novo*) mutations and pre-existing genetic variation within a population. The former is inherently constrained by the supply of new mutations, which is low in species with small contemporary population sizes (Bell, 2013; Rousselle et al., 2020). The latter has long been overlooked (Hermisson & Pennings, 2005; 2017; Pritchard et al., 2010), but assembling new adaptive genetic combinations from standing genetic variation has recently become widely recognized as a key driver of rapid adaptation (Barrett & Schluter, 2008). This is largely because standing variation of potential adaptive value is immediately available. Moreover, adaptation often has a polygenic basis, involving subtle shifts in allele frequencies across numerous loci and/or across regions of multiple small-effect loci in linkage disequilibrium rather than the fixation of single large-effect variants, allowing populations to respond more effectively to rapid environmental change (Barrett & Schluter, 2008; Matuszewski et al., 2015). In this context, introgression - the transfer of genetic material from distinct populations or closely related species through hybridization followed by repeated backcrossing - is expected to enhance standing genetic diversity and potentially fuel adaptation through natural selection on introduced alleles that have evolved under different environmental conditions (*e.g.* Pfennig, 2021; Taylor & Larson, 2019). Our review focuses on the latter process, commonly referred to as adaptive introgression.

In this review, our objective is to synthesize the current knowledge about adaptive introgression in relation to climate focussing on i) the description of the process and its demographic underpinnings, (ii) the methodological approaches to detect the process, (iii) case studies in different climate contexts, and (iv) presenting perspectives for further studies of climate-adaptive introgression and exploring its possible relevance in a conservation context. To clarify the scope of our review, it is important to note two key points. First, by definition, introgression must precede selection. However, in most systems it is difficult to determine whether an introgressed allele confers an immediate advantage or whether selection acts on it only after a period of persistence in the standing genetic variation (see Zhang et al., 2021). In this review, we consider examples of adaptive introgression when introgression was recent, without necessarily assuming that the adaptation occurred immediately. Second, we focus on non-domesticated species, since adaptive introgression in an agronomic context is already well documented (see the review by Burgarella et al. 2019 for plants, and also case studies in animals, e.g. Wang et al., 2020; Mary et al., 2022; Sarabia et al., 2025).

Before describing the process and synthesizing the available evidence, it is important to clarify our position on the current controversy regarding adaptive introgression. The contribution of adaptive introgression to overall species adaptation remains a subject of debate and polarization within the evolutionary biology community, with some researchers potentially overestimating and others dismissing its importance. Robust methods for quantifying the relative contribution of adaptive introgression to genomic adaptation are currently lacking, though some are currently under development (Jules Romieu, personal communication). Collective efforts toward developing such methodologies are essential to move beyond the current polarization and toward an objective, evidence-based understanding of the role of adaptive introgression across biota. In the absence of such standardized approaches, our objective here is to focus on the available empirical examples rather than to draw broad conclusions regarding the global prevalence. Adopting such a nuanced and cautious view is especially important when discussing adaptation to climate, given the current context of rapid global change and the projected risk of a sixth, anthropogenic mass extinction, at a time when we cannot afford to take a gamble on an overly optimistic assumption that widespread adaptive introgression will ensure climate resilience in most species.

2. Neutral and adaptive introgression: who, when and where ?

(i) Who: introgression in plants and animals

A first question concerns the conditions under which species are able to exchange genetic material, or, in other words, the level of divergence beyond which reproductive barriers preclude introgression. Such values can be critical in defining which species may act as potential donors or recipients of introgressible alleles. This question has received recent in-depth investigation through genome-wide demographic modeling across a broad range of plant and animal species (Roux et al., 2016; Monnet et al., 2025). This work has provided fundamental knowledge regarding dynamics of introgression across the continuum of divergence, providing threshold values (net divergence (d_A) of 0.3% in plants and 1.8% in animals, Monnet et al., 2025), although these values should not be considered too strictly. At similar levels of genetic divergence, plants appear to establish species barriers more rapidly than animals, consistent with more frequent reports of hybrid zones in animals than in plants (Abbott, 2017; Nieto Feliner et al., 2023). While botanists have long recognized the prevalence of hybridization in plants, it has been differentially appreciated among authors in zoology (for historical perspectives, see Mallet et al., 2007; Hedrick, 2013; Suarez-Gonzalez et al., 2018 for instance; but see also Barton & Hewitt (1985) and Mallet, 2005), particularly among species pairs with more subtle morphological differences that could have previously been overlooked by zoologists, but that became apparent upon genetic examinations (e.g. Suzuki et al., 2005; Caputi et al., 2007).

Over the past two decades, human genomics has offered a new perspective by providing compelling evidence of archaic introgression between hominins, such as Neanderthals and Denisovans (Green et al., 2010; Reich et al., 2010; Vernot & Akey, 2015, among others). Increasing empirical evidence of neutral gene flow among closely related species, including plants, humans and other animals, suggests that introgression is a widespread phenomenon (Aguillon et al., 2022). This widespread occurrence likely reflects the fact that semi-isolated species pairs are more prevalent than traditionally assumed, highlighting a persistent semi-permeability of diverging genomes to gene flow during speciation (Harrison & Larson, 2014). Following this view, rare gene flow events can introduce bursts of new genetic diversity and novel genetic combinations, even between well-diverged taxa in late stages of speciation. This outcome is especially likely when selective coefficients of adaptive loci are strong enough to surmount the effects of species barriers (Edelman & Mallet, 2021), or alternatively, balancing selection facilitating the permeability of species barriers (Gaczorek et al., 2024), further raising questions about the relative contribution of introgression in adaptation.

(ii) Where: climate as a driver of range shift and introgression

Identifying potential donor and recipient species requires considering not only their level of divergence but also the spatial context of the two species. Introgression is only possible when the ranges overlap or are close enough for dispersal to bridge the gap. Such situations give rise to demographic scenarios involving divergence with gene flow, or secondary contact that re-establishes genetic exchange between closely-related species. Past climate oscillations, especially the glacial-interglacial cycles of the last million years, have repeatedly triggered rapid range shifts across many taxa, driven by direct climatic changes, by the advance and retreat of continental ice sheets, and by indirect effects such as fluctuations in sea level. In Europe, for instance, the continent’s highly heterogeneous geography has repeatedly generated fragmented ranges with small, isolated populations during glacial periods, followed by postglacial recolonization and renewed contact among lineages during warmer periods (Hewitt, 1999; Stewart et al., 2010). Consequently, such gene flow during glacial periods or following secondary contact in warmer periods has been documented in many European animal and plant species (*e.g.* in animals: flycatchers, Ellegren et al., 2012; honey bees, Leroy et al., 2024; in plants: oaks, Leroy et al., 2017, 2020a; ashes, Heuertz et al., 2004; spruces, Zhou et al., 2024, among others). Even though geography plays a crucial role, *e.g.* through geographical isolation during glacial periods, many life history strategies likely influence the occurrence of secondary contacts. Recently, Monnet et al. (2025) reported that secondary contacts are more frequently observed in plants than in animals for instance. In turn, this pattern likely contributes to the number of well-documented cases of adaptive introgression in plants.

(iii) When: adaptive introgression through the Holocene

Although archaic introgression in hominins has been extensively studied, the most compelling examples of non-human adaptive introgression come from contemporary or recent events (Taylor and Larson, 2019). This is mostly due to methodological factors, because (i) the genetic signals of recent introgression are less eroded, (ii) they can be more readily linked to phenotypic traits, and (iii) sampling is generally easier than for ancient or historical DNA. However, another factor relates to human disturbance in the Holocene. Globalization further contributes to species introductions and long-distance dispersal of species, including the spread of pathogens and pests, thereby promoting human-mediated introgression. In a survey of nature management practitioners across Europe, 160 cases of hybridization cited (35%) involved an alien taxon (Myriam Heuertz, in preparation). A typical example involves marine species in major shipping ports, which serve as artificial environments where invasive species introduced *via* ship ballast water can hybridize with native species (e.g. Simon et al., 2020; Touchard et al., 2023). Even more strikingly, the widespread use of pesticides since the Second World War has imposed immense selective pressures on competitors in the environment, accounting for numerous well-documented cases of adaptive introgression in both animals and plants. In mice, alleles from *Mus spretus* have been introgressed into *Mus musculus* conferring resistance to rodenticides such as warfarin. This includes the genomic region of *Vkorc1*, a key warfarin resistance gene that enhances survival in *M. musculus* (Liu et al., 2015; Banker et al., 2022; see also Norris et al., 2015 for a similar example in insecticide-resistant mosquitoes). In plants, introgression of herbicide resistance alleles from agricultural crops into wild relatives has been reported for several species. For instance, introgression from cultivated maize into wild teosinte has introduced resistance alleles, allowing teosinte to persist in agroecosystems exposed to herbicides (Le Corre et al., 2020).

Beyond the direct anthropogenic impacts on current habitats and biodiversity, climate change is expected to shift many species distributions, increasing the likelihood of secondary contacts (Chunco, 2014). Such new secondary contacts will occasionally facilitate adaptive introgression, potentially rescuing species by providing alleles that help them adapt to changing conditions (Jones et al., 2018; Razgour et al., 2019; Vedder et al., 2022; Brauer et al., 2023). However, well before discussing this point, the potential negative costs of such introgression, including the evolutionary impact of the elevated selection against foreign alleles due to deleterious load and hybrid incompatibilities, should also be considered (Harris et Nelson, 2016; Todesco et al., 2016; Adavoudi & Pilot, 2021; Ramasamy et al., 2023; Leitwen et al., 2025).

3. Methodological approaches to detect adaptive introgression

Demonstrating adaptive introgression requires clear evidence of introgression (*i.e.* establishing that certain alleles originate from another species) and of adaptation (*i.e.* genomic footprints of selection and correlation with a selective driver or evidence of fitness advantages). Consequently, adaptive introgression has often been demonstrated through a combination of methods, allowing to generate independent support for both introgression and adaptation (Burgarella et al., 2019). Following a concise summary of such historical approaches, we turn to recent developments and highlight the critical role of functional and experimental work.

(i) Methods to detect introgression

Although methods used for detecting introgression have been extensively reviewed already (e.g. Martin & Jiggins, 2017; Suarez-Gonzalez et al., 2018; Burgarella et al., 2019), we provide a brief summary of key methods and how they enable differentiating a foreign ancestry from shared ancestry. A commonly used phylogenomic method is the D-statistic (commonly referred to as ABBA-BABA test) and its derivatives (*e.g.* Green et al., 2010; Malinksky et al., 2015; Martin et al., 2015). These methods are based on identifying local excess of allele sharing, beyond stochastic expectations under Incomplete Lineage Sorting (ILS). Whereas these methods are powerful in detecting genome-wide signatures of introgression, the D-statistic does not pinpoint specific introgressed regions, as its application to small genomic windows is affected by effective population size and high variability, especially in regions of low diversity or recombination, leading to potential false positives (Hibbins & Hahn, 2022; Martin et al., 2015). Over the last decade, plenty of methods based on the conceptual framework of the D-statistic but overcoming its limitations in small genomic windows have been developed, such as f4-tests (Green et al., 2010; Peter, 2016), f_{d} (Martin et al., 2015) and f_{dM} (Malinksky et al., 2015). Other phylogenetically-oriented approaches such as the use of gene tree branch lengths, as implemented in QuIBL (Hibbins & Hahn, 2022) or in Aphid (Galtier, 2024), or topology weighting, as implemented in Twisst (Martin and Van Belleghem 2017) have also contributed to pinpoint local introgression footprints, alone or in complement with *f*D and fDM (Edelman et al., 2019; Ferreira et al., 2021; Yardeni et al., 2025; among others). In addition, several population genomics-oriented methods, including local ancestry inference tools like RFMix (Maples et al., 2013) or ChromoPainter-FineStructure (Lawson et al., 2012) and genome polarization approaches like in diem (Baird et al., 2023), are commonly used to identify introgressed tracts.

(ii) Methods to detect selection

While detecting introgression is crucial, it alone does not distinguish neutral from adaptive introgression. Indeed, detecting selection footprints in introgressed regions involves identifying genomic signatures that deviate from neutral expectations, therefore suggesting positive selection acting on the introgressed alleles. Most approaches are population genomics-oriented, either detecting selection by comparing patterns of genetic variation along the chromosomes within populations, or by looking at population differentiation. Within populations, a plethora of methods are based on different signatures of selection in genomic regions surrounding its target (*i.e.* selective sweeps), including locally reduced nucleotide diversity (π), skewed allele frequency spectra (excess of low- or high-frequency alleles, Tajima’s D), extended haplotype homozygosity (e.g. iHS, XP-EHH, Klassmann & Gautier, 2022) or increased linkage disequilibrium (Alachiotis et al., 2012). Among populations, loci exhibiting elevated allele frequency differentiation between populations (e.g. F_{ST} or X^TX outliers, Günter & Coop, 2013) or genotype-environment association (GEA) methods (BayEnv, BayPass, LFMM, or RDA, Günter & Coop, 2013, Gautier et al., 2013; Frichot et al., 2013; Forester et al., 2018) that identify statistical associations between allele frequencies and ecological variables, suggest that introgressed variants contribute to local adaptation. Additionally, comparative genomics methods, such as the McDonald-Kreitman test and related approaches (McDonald & Kreitman, 1991), complement these population genomic-oriented methods by contrasting patterns of polymorphism and divergence to infer positive selection in genes within the introgressed regions.

(iii) Advancing methods for jointly detecting introgression and selection

Methodological developments have recently allowed shifting towards jointly detecting introgression and selection on introgressed loci. Compared to separate approaches, integrated analyses are expected to better capture subtle or overlapping signals and to mitigate confounding factors such as incomplete lineage sorting and complex demographic histories. To be applicable, most of these methods require sequence data from representatives of both the recipient and the donor species, including introgressed and non-introgressed populations. Racimo's Q95(w, y) summary statistic (Racimo, 2017) was specifically designed to identify regions with high-frequency derived alleles that are shared between the donor and recipient population, while these alleles are at low frequency in the non-introgressed sister population, providing a simple yet effective way to detect adaptive introgression (Fig. 1). Contrary to the other methods, VolcanoFinder (Setter et al., 2020) does not require data from the donor, since it identifies "introgression sweeps", a volcano-shaped pattern due to an excess of intermediate-frequency polymorphisms around the positively-selected site within the data from the recipient population alone (Setter et al., 2020). Empirical use of VolcanoFinder on Tibetan hominin genomes has revealed not only introgression at the *EPAS1* gene - a textbook locus of adaptive introgression (Huerta-Sánchez et al., 2014; Zhang et al., 2021)-, but also at other loci, highlighting the oligogenic nature of adaptation to hypoxia through archaic human introgression (Ferrarretti et al., 2024). Genomatnn (Gower et al., 2021) and MaLAdapt (Zhang et al., 2023) employ deep learning and machine learning approaches, respectively, to classify genomic windows as resulting from adaptive or non-adaptive introgression. Concretely, genomatnn uses deep learning with convolutional neural networks trained on simulated genotype matrices, specifically designed to distinguish adaptive introgression from confounding neutral processes and demography, as well as other forms of selection, in order to identify adaptive introgression on empirical data. MaLAdapt (Zhang et al., 2023) uses a machine learning approach that combines multiple statistics to distinguish adaptive from non-adaptive introgression. Although these tools were initially developed in the context of human evolution and have so far seen limited application to empirical data in other systems, recent simulation-based evaluations across diverse evolutionary scenarios suggest that their performance is highly sensitive to model assumptions and demographic contexts (Romieu et al., 2025). Notably, simpler approaches such as Racimo's Q95(w, y) summary statistic can perform comparably - or even outperform these learning-based methods - in terms of robustness and accuracy (Romieu et al., 2025). Despite its conceptual simplicity, Q95(w, y) remains one of the most effective tools currently available for detecting adaptive introgression.

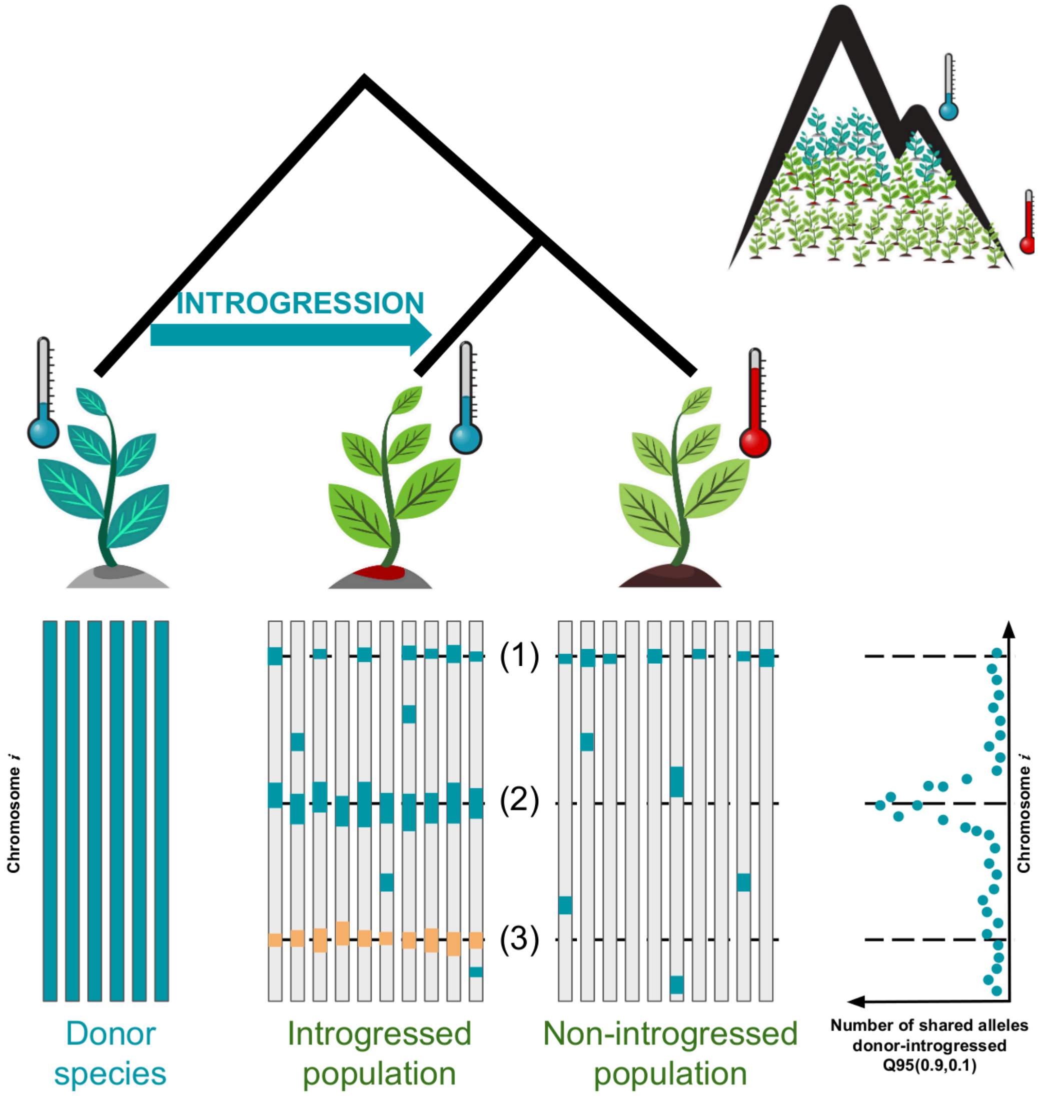

Figure 1. Theoretical example of adaptive introgression contributing to cold tolerance at high altitude, illustrated using Racimo's Q95 summary statistic. *Each vertical bar represents a copy of a given chromosome i, with blue segments indicating genomic regions carrying the same alleles as the donor population. The Q95 statistic (Racimo et al., 2017) is computed across the chromosome to detect signals of adaptive introgression, with values plotted along its length. Three illustrative cases are highlighted: (1) A region showing shared alleles in both introgressed (high elevation) and non-introgressed (low elevation) populations, resulting in no elevation of the Q95 summary statistic, potentially reflecting high incomplete lineage sorting (ILS) rather than selection. (2) A candidate region with a pronounced Q95 peak where donor alleles are at high frequency in the introgressed (high-altitude) population, consistent with positive selection for cold-adaptive introgressed variants. (3) A region outside of introgressed segments displaying a potential hard selective sweep within the focal population (orange) rather than from introgression from the donor species (blue), resulting in no elevation of the summary statistic.*

(iv) The crucial importance of high-quality gene annotations

An important, albeit often neglected, aspect is the integration of high-quality functional annotation. However, high-quality gene annotation are accessible for a growing number of species (e.g. NCBI, 2015: 276, 2025: 1406, a 409% increase), as well as through annotated metabolic pathways (e.g. +80 ‘KEGG organisms’ species/month, Kanehisa et al., 2025) or expression data (e.g. from RNA-seq or ATAC-seq). All together, these approaches can help assess whether the candidate regions could indeed host genes that affect relevant traits. The favourable trend in terms of well-annotated species genomes is expected to accelerate over the next decade, driven by advances in gene annotation tools, including the emergence of deep learning-based strategies that have already started to increase the accuracy of gene prediction (Chen *et al.,* 2024; Davison et al., 2025). Such high-quality investigations will likely surpass precise gene ontology (GO)-term enrichment analyses, which have become increasingly popular over the past decade or two for interpreting functional patterns in genomic data. GO-term analyses are, however, often affected by multiple sources of bias, including uneven annotation quality among species (experiment-based *vs.* bioinformatic annotations), overrepresentation of well-studied genes, the use of overly broad or redundant terms (e.g. Gaudet & Dessimoz, 2016; Strielkov et al., 2025). Major methodological flaws in enrichment testing have been reported in most studies, leading to widespread reproducibility issues (Yon Rhee et al., 2008; Wijesooriya et al., 2022). Despite advances continuing to be made to solve some issues (e.g. Koopmans, 2024, Valverde et al., 2025), some inherent challenges of enrichment analysis will, however, remain, including the fact that such approaches require making strong assumptions regarding the genetic basis of adaptation. For example, achieving significant enrichment in large gene families typically assumes a polygenic basis for adaptation, even though a single gene within a large family may still play a pivotal adaptive role. Consequently, while gene enrichment analysis can theoretically offer useful insights in the context of adaptive introgression, its outputs alone should be interpreted with caution.

(v) The critical need for experimental validation

Direct experimental evidence of enhanced fitness of introgressed *versus* non-introgressed individuals is the most compelling support for adaptive introgression. Such investigations typically involve linking genetic variation to phenotypic traits and demonstrating that these traits improve performance - such as increased survival, reproduction, or stress tolerance - in the laboratory or in (semi-)natural environments, such as in common garden or reciprocal transplant experiments. Textbook examples of adaptive introgression in adaptation of trees to changed climatic conditions were at least partially based on such common garden strategy (*e.g.* Suarez-Gonzalez et al., 2016; Leroy et al., 2020b; Martha Rendón-Anaya et al., 2021). Powerful, field-based experiments, including common garden or reciprocal transplant studies, are often difficult to implement in practice, as they tend to be time-consuming, expensive, and particularly challenging for non-model, long-lived, or threatened species (Taylor & Larson, 2019). Albeit crucial, such long-term experiments are further constrained by several factors, including the short-term grant funding system, which threatens continuity and limits the development of new experimental setups, as well as by additional concerns such as the potential biological risks associated with such transfers (e.g. conservation-related, long-distance pathogen dispersal and evolution, etc. Leroy et al., 2016; Ramírez-Castañeda et al., 2022).

4. Case studies of adaptive introgression in a climate context

To identify cases of adaptive introgression in relation to climate, we conducted a systematic search in Pubmed with the terms *adaptation AND introgression AND climate* yielding 15,318 studies published between 1957 and 2025, which when refined to *("adaptive introgression"[Body - All Words] AND "climate"[Body - All Words]) NOT "crop"[Body - All Words]* narrowed down to 353 studies published between 2007 and 2025 (search conducted on 12 November 2025). The results cover a broad range of taxa, both in terms of life forms and life history strategies (Figure 2, Table 1), as well as in terms of climate zones and climatic covariates. Climate parameters are widely hypothesized to act as potential drivers of introgression and to shape the associated species response traits. Selected example cases from the literature review, along with some complementary searches on these cases, are presented below, sorted according to their climatic covariates. The section aimed to highlight common climatic drivers of adaptive introgression, but is probably not exhaustive. Other climate-relevant putative drivers exist, *e.g.* in the marine environment, but are less well understood, such as sea level change resulting in adaptive introgression among *Acropora* coral species (Mao et al., 2018). The cited examples illustrate frequent co-introgression of adaptation-relevant genes, for example of temperature, precipitation and phenology-related genes (Feng et al., 2025; Leroy et al., 2020).

(i) Adaptation to drought or dry environments

Adaptation to drought or dry environments is a frequent requirement under climate change. In the toad *Anaxyrus canorus*, a genomic analysis of introgression patterns and a GWAS analysis with tadpole development traits identified 10 genomic locations including LPIN3, a lipid metabolism gene, potentially involved in desiccation tolerance. This gene was present in genomic regions of high among-lineage divergence across three contact zones, but was affected by introgression at one of these contact zones (Maier et al., 2024). In mammals, adaptation to drought involves temperature regulation that is tightly linked to skin and hair traits. This is exemplified in indigenous goats in Southwest Asia adapted to desert climate, in which the KITLG region affecting hair follicles and related to heat loss capacity was found to be introgressed. The possible origin of this drought-adaptive KITLG region lies in the Nubian ibex from which it introgressed into domestic goats, and subsequently into Southwest Asian wild animals (Asadollahpour Nanaei et al., 2023). Similarly, in plants, there are also examples of introgression in relation to drought adaptation, especially in forest trees. In *Eucalyptus grandis*, provenances showed extensive interspecific introgression in genomic regions enriched for defense response and signalling genes in response to increased aridity (Mostert-O'Neill et al., 2021). In a complex of three allopatric spruce species in China, introgression of root-morphology and stress tolerance genes from the drought-adapted *Picea crassifolia* into the threatened *P. meyeri* likely enhanced the environmental niche and ecological plasticity of the latter (Feng et al., 2025). Climate-driven interspecific gene flow associated with hyperarid desert habitats is also exemplified by plants of the genus *Tillandsia,* where introgression in *T. landbeckii* is associated with an expansion of its ecological niche (Stein et al., 2023).

(ii) Adaptation to cold climate gradients

Adaptation to cold environments has been facilitated by adaptive introgression in both plants and animals. Among mammals, the snow sheep *Ovis nivicola*, a wild herbivore inhabiting cold and alpine habitats of northeastern Siberia, shows evidence of introgression with the high-altitude argali sheep (*Ovis ammon*) and Dall sheep (*Ovis dalli*), likely resulting from contact during the Pleistocene. The introgressed genomic segments include genes associated with immunity, adipogenesis and morphology-related traits, representing potential targets of adaptive introgression. Notably, adipogenesis-related genes displayed introgression across several species boundaries in sheep and were under selection in snow sheep (Upadhyay et al., 2021). Another interesting case of adaptation to high altitude concerns Myospalacinae, a group of subterranean rodents. In this group, low-altitude Gansu zokors (*Eospalax cansus*) have introgressed cardiovascular-related genes associated with hypoxia adaptation from the high-altitude plateau zokors (*Eospalax baileyi*), which likely facilitated their adaptation to higher-altitude grass-land ecosystems of the Qinghai-Tibet Plateau (Kang et al., 2024). In bird species of the genus *Stercorarius,* colonisation of polar environments in Southern hemisphere was made facilitated by hybridization, with signals of selection in hybrids for genes involved in fatty-acid metabolism (RBP7 and C3orf38, Jorquera et al., 2025). As in animals, several examples were also observed in trees. In an extensive hybrid zone between *Pinus strobiformis* and *P. flexilis* across western North America, introgressed variants from the cold-tolerant *P. flexilis* were preferentially retained along freeze-susceptible environmental gradients, while background variants were favoured along gradients related to water availability (Menon et al., 2021). Adaptive introgression also likely enabled the cypress *Cupressus duclouxiana* to expand its range to higher altitudes on the Qinghai-Tibet Plateau. Indeed, northern populations of *C. duclouxiana* exhibit 16 genes under selection, enriched for stress tolerance functions, introgressed from the related high-altitude *C. gigantea* (Ma et al., 2019). In the European white oaks, *Quercus petraea* populations from cooler environments along latitudinal and altitudinal gradients exhibit a higher level of introgression from *Q. robur.* Genomic regions introgressed from *Q. robur* involved in adaptation to these environments were found associated with both water stress and phenology (leaf-unfolding in common gardens) and include several genes controlling stomatal responses, such as RopGEF1 and PBL10 (Leroy et al., 2020b).

(iii) adaptation to climate warming

Adaptive introgression conveying adaptation to climate warming is exemplified in species that expand their ranges from cold or harsh climates into milder areas. An interesting case is the snowshoe hare (*Lepus americanus*), widely distributed in the boreal climate zone in North America. While the species typically develops white winter fur, some populations exhibit brown winter camouflage due to a selective sweep at the Agouti pigmentation gene, which is introgressed from black-tailed jackrabbits (*L. californicus*, Jones et al., 2018). While a hybridization pulse between these species has been dated to the end of the last glacial maximum, the selective sweep was probably more recent and facilitated south-ward range expansion into milder climate (Jones et al., 2020). In damselflies, hybridization with the Iberian *Ischnura graellsii* enabled niche expansion of *I. elegans* into the Iberian peninsula (Wellenreuther et al., 2018). Introgression of warm-advantageous traits may reduce the carrier population’s vulnerability to contemporary climate warming. Demonstrating this process is delicate but has been done in an altitudinal gradient in the *Melanotaenia* rainbowfish species complex in the Australian Wet Tropics in which high-altitude narrow endemic lineages hybridizing with a widespread low-altitude congener had reduced vulnerability to projected climates compared with pure narrow endemics. The hybrid lineages displayed introgressed regions enriched in genes with regulatory functions on heat shock proteins and cellular responses to thermal stress (Brauer et al.,, 2023). In the Sino-Himalayan fulvetta bird species complex, introgression of alleles linked to warm-humid tolerance from *Alcippe hueti* into the temperate-adapted higher-altitude *A davidii*, *e.g.* KBTBD2 mediating cellular response to heat stress, was associated with reducing climate change vulnerability of the latter species (Zhang et al., 2025). Adaptive introgression during range expansion conveying adaptation to warm climates can also be detected as balancing selection, which is the case in the kleptoparasitic spider *Argyrodes lanyuensis* endemic to the area between the subtropical Taiwan and the wet tropical Philippines, in which the climatically intermediate Green island was colonised by a hybrid lineage featuring stress-tolerance genes under balancing selection (Responte et al.,, 2025). A plant example concerns the southward range expansion of the orchid *Paphiopedilum wenshanense* in which introgression from *P. concolor* occurred preferentially in the southernmost populations and was associated with climatic covariates such as increased rainfall seasonality and annual mean temperature (Jiang et al., 2025).

(iv) Climate adaptation through phenology

Adaptation of phenology associated with climatic conditions frequently becomes necessary as a consequence of migrating to new latitudes. For example, in migrating fish species such as Atlantic salmon, run time, i.e., the timing of return to natal rivers for spawning is a highly fitness-relevant trait. In North American Atlantic salmon, both early and late run time were associated with the transatlantic introgression of a large structural variant and maturation-associated genes previously characterised in Atlantic salmon including ppfia2, a migration-timing gene conserved across vertebrates (Beck et al.,, 2025). In plants, a typical example is the European aspen, *Populus tremula*, in which northern Scandinavian populations are homozygous for a ~500 kb in chromosome 10 introgressed from more Eastern populations and carrying two *Flowering Locus T* homologs, photoperiod-relevant genes that contribute to adaptation to the short growing seasons characteristic of Northern Scandinavia (Rendón-Anaya et al., 2021). A similar case of phenology-relevant introgression conveying adaptation to high latitude climates concerns weedy teosintes found in maize fields of France and Spain. These weeds were found to originate from *Zea mays* ssp. *mexicana* race “Chalco,” a weedy teosinte from the Mexican highlands, and carried ZCN8, a major flowering time gene introgressed from the high latitude Dent maize grown in Europe, along with other introgressed regions conferring herbicide resistance (Le Corre et al., 2020).

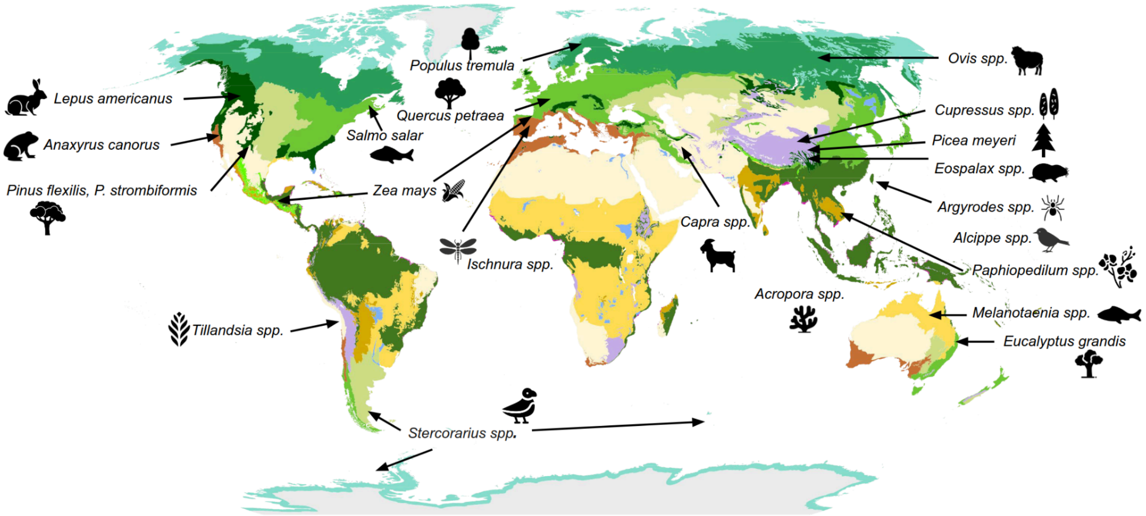

Figure 2. Example cases of climate-relevant adaptive introgression described in the paper. *The background map represents Terrestrial biomes of the world according to Olson & Dinerstein (1998) and used by the WWF and Global 200, downloaded from Wikipedia (CC BY-SA 3.0). Free icons were downloaded from www.flaticon.com.*

5. Perspectives regarding adaptive introgression

(i) Past adaptive introgression and diversification

Adaptive introgression is one of the evolutionary biology topics that lies at the interface between micro- and macroevolution. Even the methods we reviewed are typically oriented toward either population genomics or phylogenomics, reflecting a conceptual and methodological division in the community that can limit our understanding of adaptive introgression. Bridging micro- and macroevolutionary perspectives is an important step toward understanding how adaptive introgression contributes to species diversification. Comparative genomic studies investigating large sets of species pairs along a continuum of divergence are increasingly common (e.g. Stankowski et al., 2019; Shang et al., 2023; Postel et al., 2025; Schield et al., 2025), providing a robust framework to quantify how reproductive isolation accumulates across lineages. Building on such large-scale comparative datasets, future research could integrate population-level analyses of adaptive introgression to identify when and how introgressed alleles persist or vanish across different stages of divergence. Developing this integrative approach, combining population genomics, functional, ecological, and phylogenomics, will help trace the fate of introgressed alleles from local adaptation to long-term lineage diversification. Fine-scale demographic inference, ecological context, paleogenomics and experimental validation can clarify the selective mechanisms underlying introgression, while comparative phylogenomic frameworks and diversification models can test whether introgression systematically promotes speciation and potentially fuels evolutionary radiations (e.g. Meier et al., 2017; Svardal et al., 2020; Qian et al., 2023; Yardeni et al., 2025). Such work is especially important in a climate context, since at a macroevolutionary scale, the role of climate heterogeneity in speciation has been well documented across numerous plant and animal taxa, with generally higher diversification rates observed in warm periods or regions (e.g. Mittlebach et al., 2007; Quintero & Jetz, 2018; Rangel et al., 2018; Condamine et al., 2019; Juve et al., 2025).

(ii) Genomic offset, adaptive introgression and rescue

Genomic offset is an emerging approach for predicting future maladaptation under rapid environmental change, especially climate change (Fitzpatrick & Keller, 2015; Rellstab et al., 2021). The rationale of these methods is to estimate the potential mismatch between current and future environmental conditions, through the distance between the current and future optimal genetic composition. Whereas this approach is not able to account for alleles that are not already introgressed in the current genetic composition (*i.e.* those not already identified as part of the adaptive genetic component through genotype-environment associations), it would still be theoretically possible to compare genomic offset maps of closely related species to identify potential sources and predict directions for future adaptive introgression. A similar approach has been used to predict source and sink populations for evolutionary rescue potential in the bat species *Myotis escalerai* and *M. crypticus* (Razgour et al., 2019), and also to predict sources and destinations of future potential invasions (Camus et al., 2024). In this context, if one taxon shows a lower genomic offset under projected future conditions, it could act as a potential donor species and serve as a genetic rescuer. If and when such gene flow will indeed happen, either naturally or through human-assisted movement, these alleles are expected to introgress, reducing their genomic offset of the recipient species, providing a genomic rescue. As a result, combining offset-based vulnerability assessments with introgression analyses could provide a powerful framework for forecasting adaptive responses in changing environments.

(iii) Community-level investigations

Investigating adaptive introgression has important consequences for conservation and management in the face of climate change and land-use change. Recognizing this role does not mean adopting a simplistic view of adaptation. Adaptive introgression generally focuses on single species investigations, while the fitness of this species is often associated with a wide community of organisms, from closely associated species (gut microbiota, plant phyllosphere, etc.) to more distant interactions in complex ecosystems. Although estimating the precise contribution of adaptive introgression to adaptation is currently an important step forward (Jules Romieu, personal communication), current research mainly targets single species. It is now time to explore how entire communities of symbiotic organisms - the so-called super-organisms - adapt over short timescales, and to better understand the true contribution of adaptive introgression at a broader scale. For many organisms, sequencing whole individuals (*e.g.* insects) or specific organs (*e.g.* gut, leaves) can provide valuable information on microbial diversity through metagenomic approaches. In fact, most studies focused on a single species begin by mapping sequencing reads to a single reference genome, discarding all other DNA. Generating genomic resources (metassembling) allows investigating how these other species adapt, including the microbiome itself. Environmental DNA (eDNA) approaches are expected to become a key future direction in order to estimate the contribution of adaptive introgression at the level of community genomes.

Author Contributions

TL prepared the first drafts of sections 1, 2, 3, and 5. MH carried out the literature search related to adaptive introgression in a climate context and wrote the associated section 4. Both authors contributed to the revision and approval of the final manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

No new data was generated.

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Table 1: Cases of climate-relevant adaptive introgression described in this paper.

Species / Taxa	**Phylum /life form**	**Genetic data/marker and sampling**	**Methods used for the detection of introgression**	**Methods used for the detection of selection**	**Functional evidence**	**Climate variables, phenotypes or fitness**	**References**
Acropora sp.	Corals	Whole-genome sequences n=5, one genome per species (*Acropora digitata*, *A. echinata*, *A. gemmifera*, *A. subglabra*, *A. tenuis*)	ABBA-BABA statistic, speciation with isolation and speciation with migration modeling, cluster analysis for co-introgressed genes	dN/dS, GO terms enrichment	GO terms analysis, literature searches	sea-level change (rise)	Mao et al., 2018
Alcippe spp.	Birds	Whole-genome sequences n=78 across 3 species, *A. davidi*, *A. fratercula* and *A. hueti*	Dstatistics, FILET	Selective sweep analysis, GEA with climate, genomic vulnerability with niche models, genomic offset, forward simulations, genetic connectivity	GO terms analysis, functional annotation, literature searches	Adaptation to warm-humid conditions and reduction of climate vulnerability for temperate-adapted species	Zhang et al., 2025
Anaxyrus canorus	Amphibian	Reduced representation (ddRAD-seq) n=535 tadpoles mapped on transcriptome, 3 contact zones involving pairs of a total of 4 lineages	Islands of divergence with dendropy and regions of admixture with genomic cline analysis (bgc)	Depletion for outliers (highly diverged or highly admixed), GWAS with tadpole traits	GO terms enrichment, literature searches	dessication, regulation of tadpole growth during dessication	Maier et al., 2024
Argyrodes lanyuensis	Spider	Reduced representation (RAD-Seq), n=130 from 15 localities on 9 islands	ASAP species delimitation and D statistics	natural selection by comparative population genomic analysis, CEGA	Manual annotation, literature searches	Hybrid lineage on Green island with intermediate climate between tropical and subtropical climates of parentals	Responte et al., 2024
Capra sp.	Mammalia	Whole-genome sequences n=50 ancient, n=211 domestic, and n=72 wild Capra genomes	ADMIXTOOLS, f3-statistics, D statistics	Selective sweep & FST outlier analysis	annotation based on reference genome, literature searches	adaptation to drought	Asadollahpour Nanaei et al., 2023
Cupressus gigantea/ C. duclouxiana	Trees	Transcriptome (RNA-Seq) n=30 Cupressus duclouxiana, n=35 C. gigantea trees	D, fdM, dxy statistics	HKA test, ecological niche modelling	GO terms enrichment, literature searches	Adaptation to high altitude	Ma et al., 2019

Eospalax baileyi, E. cansus	Mammalia	Whole-genome sequences (low coverage), n=230 individuals from 19 populations, high and low-altitude species	D and fd statistics	Selective sweep detection (low π), high F_{ST}	GO terms enrichment, literature searches	Adaptation to high altitude, adaptation to hypoxia	Kang et al., 2024
Eucalyptus grandis	Trees	Genetic marker datasets (SNP array 60K) n=362 individuals from 33 provenances, and five outgroup species with n=10-18/species	Efficient Inference of Local Ancestry (EILA) R package	Environmental association with LFMM	GO terms enrichment, literature searches	adaptation to drier climates, with introgressed provenances at lower dry period average precipitation	Mostert-O'Neill et al., 2021
Ischnura elegans, Ischnura graellsii	Insects	Genetic marker datasets (SSRs), n=29 *I. graellsii*, n=208 *I. elegans*, from 14 populations	Admixture proportions compared with simulated hybrids	Niche modelling	Niche breath of introgressed vs. pure populations	Niche expansion	Wellenreuther et al., 2018
Lepus americanus/L. californicus	Mammalia	Whole-genome sequences n=80 from 4 US regions	PhylonetHMM, simulation of hybridization pulse with SELAM	Simulation-based inference of TMRCA for the Agouti region	Annotation based on reference genome, literature searches	Expansion into mild climate range	Jones et al., 2020
Melanotaenia spp.	Fish	Reduced representation (ddRAD-Seq), n=344 fish from five species	D, f4-ratios and fdM statistics (Dsuite)	GEA with climate, genomic vulnerability with niche models, genomic offset	GO terms enrichment, literature searches	Adaptation to climate warming in altitudinal/temperature gradient	Brauer et al., 2023
Ovis nivicola, *Ovis* sp.	Mammalia	Whole-genome sequences n=6 O. nivicola, n=1 O. dallii, n=1 O. ammon	F4 statistics, TREEMIX, relative node depth (RND) in phylogeny	Branch-site model in CODEML and Fay & Wu's H test for positive selection	Annotation based on reference genome, literature searches	Cold adaptation (to subarctic climate)	Upadhyay et al., 2021
Paphiopedilum wenshane, P. concolor	Orchid	Reduced representation (RADseq), n=81 *Paphiopedilum wenshane,* n=9 P. concolor, n=10 P. bellatum	neighborNet, ABC demographic modelling, gene flow estimatew with divMigrate	Environmental and flower morphology correlates with introgressed regions	GO terms enrichment, literature searches	Higher introgression in more southern latitudes correlating with warmer and moister climates	Jiang et al., 2025
Picea asperata, P. crassifolia, P. meyeri	Trees	Transcriptome (RNA-Seq) n=114 from 21 populations of 3 species	D-suite, TREEMIX, fdM	Selective sweep analysis, GO-terms enrichment, RDA with environment, species distribution	Functional annotation, GO terms enrichment, literature searches	Adaptation to drought, photoperiod	Feng et al., 2025

				modelling			
Populus tremula lineages	Trees	Whole genome sequences n=411 from 7 countries	fdM and df statistics, ELAI	iSAFE (integrated selection of alleles favored by evolution)	Annotation based on reference genome, lliterature searches	Latitudinal gradient, shorter growing season	Rendón-Anaya et al., 2021
Quercus petraea	Trees	Whole-genome sequences (poolseq) 18 populations with 1pool/pop across altitudinal and latitudinal gradients, 1 pop each of Q. petraea, Q. robur, Q. pyrenaica, Q. pubescens	TREEMIX, f3 statistic	GEA (Baypass) outlier identification (temperature, precipitation) and GPA (leaf unfolding date)	Manual annotation, common gardens, literature searches	Latitudinal and altitudinal gradients	Leroy et al., 2020b
Salmo salar	Fish	Genetic marker datasets (SNP array, 220k SNPs), n=297 individuals from 11 populations	based on literature	pRDA, LFMM for genotype-phenotype association	GO terms enrichment, literature searches	Climate warming, timing of long-distance marine-to-river migration, genomic offset	Beck et al., 2025
Stercorarius spp.	Birds	Whole-genome sequences n=111 individuals from 21 locations, 3 species	D and f4 statistics	Sweep Detection (RAiSD), LD patterns (XP-nSL)	GO enrichment	Adaptation to extreme environments facilitates polar colonisation	Jorquera et al., 2025
Tillandsia spp.	Herbaceous plants	Reduced representation (GbS, plastome) n=489 individuals from 3 species + 1 outgroup	TREEMIX	niche modelling	niche broadening with introgression	Adaptation to extreme aridity	Stein et al., 2023
Zea mays (teosinte)	Herbaceous plants	Whole-genome sequences (SNP array, 50k SNPs) n=70 accessions French teosintes, + published data of n=40 Spanish teosintes, n=314 acc. *Z. parviglumis*, n=332 acc. *Z. mexicana* (28, 29), n=94 *Z. mays* landraces, n=155 *Z. mays* inbred lines	F4 statistics, TREEMIX	Differentiation scan (pcadapt), ELAI, SNP outliers mapping to genome	Annotation based on reference genome, literature searches	Adaptation of flowering time to temperate climate (shorter in introgressed temperate-adapted teosinte)	Le Corre et al., 2020