

# What about Adaptive Introgression? The Genomic Revolution Is Shaping Scientific and Public Perception

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## Article

**Keywords:** Adaptive introgression, Genetic miscegenation, Perception, Sentiment analysis, Systematic review

**Posted Date:** November 11th, 2021

**DOI:** <https://doi.org/10.21203/rs.3.rs-1041127/v1>

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# Abstract

Genetic miscegenation was historically perceived as a maladaptive process or even an imperfection of nature. However, through adaptive introgression, some species can share genes associated with well-adapted traits. Current scientific perceptions on the benefits of adaptive introgression can help to clarify how these paradoxes condition scientific progress and influence public beliefs and decision-making. We carried out a systematic review and bibliometric analysis using artificial intelligence on adaptive introgression evidence. The genomic revolution provided an exponential growing of evidence predominately interpreted as beneficial for species adaptation. We show that this remarkable increase on publications influences public perception in the medium-long term. Despite an initially emotional response, peoples' final opinion tends to incorporate science-based evidence, although prejudices seem to influence peoples' polarity opinion. We argue that developing the knowledge on adaptive introgression will allow to scientifically refute theories that promote genetic "purity", used to justify racism and other forms of discrimination.

## 1 | Introduction

Introgression can be a key evolutionary mechanism allowing species to incorporate portions of the genome of another species through horizontal gene transfer (Anderson and Hubricht, 1938, Arnold and Kunte, 2017). Through repeated interbreeding a species can receive genes from another species, eventually resulting in fitness changes (Cahill et al. 2015, Djogbénu et al. 2008, Enciso-Romero et al. 2017, Gagnaire et al. 2009) - a natural evolutionary phenomenon known as adaptive introgression (Pfennig, 2021). Methodological developments through High-Throughput Sequencing and bioinformatics approaches led to an increase in the scientific evidence for the spread of adaptive introgression (Pfeifer and Kapan, 2019, Taylor and Larson, 2019) across different geographic areas (Brower, 2018, Giska et al. 2019, Ma et al. 2019, Morales et al. 2018, Suarez-Gonzalez et al. 2018b) and taxonomic groups (Maddamsetti and Lenski, 2018, Maxwell et al. 2019, Nader et al. 2019, Paetzold et al. 2019, Silvert et al. 2019). It is not always the case that introgressed populations have an adaptive advantage derived from introgression (Harris and Nielsen, 2016). However, when it does occur, they can potentially jump to a new adaptive optimum, thus surpassing intermediate evolutionary steps (Ballerini et al. 2012).

Several studies recognise adaptive introgression as beneficial for species fitness (Acosta and Premoli, 2018, Aeschbacher et al. 2017, Hohmann and Koch, 2017, Horn et al. 2018, Lehnert et al. 2019, Ma et al. 2019, Paun et al. 2016, Semenov et al. 2018). Possible reasons for the benefit of introgression are the potential of adaptive introgression for promoting individual survival (Hejase and Liu, 2016, Norris et al. 2015), range expansion (Whitney et al. 2015), species divergence (Morales et al. 2017), evolutionary rescue (Quigley et al. 2019) and adaptive radiation (Poelstra et al. 2018, Zhang et al. 2016). Additionally, there is multiple evidence of advanced-generation hybrids whose backcrosses exhibit adaptive traits beyond the ancestral phenotypic range (DiBattista et al. 2016, Salazar et al. 2008, Scascitelli et al. 2010), sometimes leading to hybrid speciation (Aleksic et al. 2018, Brower, 2018). This is a strong argument to support that gene flow between sympatric lineages (species, population, breeds, etc.) may represent an

adaptive strategy for survival under extreme environmental conditions (Hamlin and Arnold, 2014, Martin et al. 2016, Martin et al. 2006, Suarez-Gonzalez et al. 2018a).

On the other hand, introgression has been historically understood as a homogenizing process (Latch et al. 2006, Oliveira et al. 2008), which can influence the long-term viability of species through genetic swamping (Maguilla et al. 2017). Some scientists argue that interspecific gene flow may counteract local selection pressures, decreasing the fitness of diverging populations by introducing alleles from outside the local adaptive range (outbreeding depression; Bolnick and Nosil, 2007, García-Ramos and Kirkpatrick, 1997, Maguilla et al. 2017). Moreover, other scientists considered natural hybridization as a violation of species integrity, a maladaptive process or an unexpected imperfection of Nature (Llopart et al. 2014, Lowe et al. 2015).

These contrasting views reveal a controversy over the merits of adaptive introgression. In fact, a number of studies have already suggested that philosophical and cultural background may be behind the negative prejudices of the scientific community towards natural hybridization (Arnold et al. 2012). Paterson (1985) highlights such prejudice even in terms of semantics noticing how appreciative are “words such as “pure”, “purebred”, “thoroughbred” and how pejoratives are those like “mongrel”, “bastard”, “half-breed” or “hybrid” with the role of ‘protecting the integrity of species’. Assessing scientific perception of the benefits of genetic miscegenation through adaptive introgression is important for better understanding which factors, beyond scientific evidence, condition scientific progress. Bias in perceptions of the merits of genetic miscegenation directly or indirectly influences fields like conservation biology (Biermann and Mansfield, 2014, Chan et al. 2019, Genovart, 2008), animal husbandry/agriculture (Henkel et al. 2019), human relations and social policies (Bethencourt, 2013, Baker, 2016, Fredrickson, 2002).

In animal husbandry and agricultural production the demand for pure variants, with the most desirable traits, is nowadays seen as development and progress (Henkel et al. 2019). Paradoxically, although the promotion of genetic variation is a key conservation goal (Chan et al. 2019), the protection of pure lineages/species remains at the forefront of conservation priorities (Biermann and Mansfield, 2014, Genovart, 2008). From a social point of view, biases against genetic miscegenation were historically manifested through policies promoting forced sterilizations, segregation, direct medical killings and lab experiments in human beings (Schoen, 2005), as well as anti-miscegenation laws, prohibiting marriage between people from different “races” (Baker, 2016).

Understanding both scientific and public perception of the evidence for adaptive introgression is essential for determining how the evidence can shape public opinion and emotions towards genetic miscegenation (Damasio and Carvalho, 2013) and how it can influence decision makers (politicians, conservationists, lobbyists, human rights organizations, etc.).

However, inferences of perception patterns about scientific facts are nowadays particularly hard to obtain due to the growing amount of scientific publications and the huge number of opinions derived therefrom that circulate in official documents and conventional and social media. Conventional approaches for obtaining scientific data about perceptions, such as social surveys, can be costly and time-consuming,

especially when targeting large audiences and broad spatial and temporal coverages. These approaches can also be difficult to implement because they assume an active process with strong subjectivity bias, namely due to perceivers' experience, motivation and how they are feeling when processing the information (Sacks and Gary, 2012, Dange, 2016). This is particularly evident in the phenomenon of "perceptual defence", whereby perceivers only see what they expect to see to support their own beliefs (Christianson et al. 2017).

To help overcome these limitations, artificial Intelligence (AI) tools, and specifically deep learning techniques, have been increasingly adopted to analyse large amounts of online data (Yang et al. 2019). Deep learning relies on mathematical algorithms endowing machines with intelligent behaviour to learn patterns and adapt such learning processes to new data. By doing so, deep learning algorithms gain the ability to automatically process and identify similarities between patterns of digital information, such as texts or images (Yang et al. 2019). In the case of textual data, sentiment analysis has become a promising technique to analyse the polarity of written sentences or words as positive, negative or neutral (Ainin et al. 2020). When supported by robust data and adequate meaning, sentiment analysis can serve as a proxy to verbal behaviour, attitudes, and emotions, which are useful for understanding the perceptions and opinions of writers about different topics (Ainin et al. 2020).

Here, we aim to understand the extent to which adaptive introgression has been receiving attention in scientific literature and the way the scientific community and the public perceive scientific discoveries relating to adaptive introgression. Specifically, we aim to answer the following questions: (1) What is the scope and evolution of knowledge about adaptive introgression? (2) What do the scientific community and general public think about adaptive introgression? (3) Which sentiments can be triggered in the public as a reaction to evidence of adaptive introgression? Based on our findings we suggest avenues for fostering progress of adaptive introgression and adjust its course in Evolutionary Biology.

## **2 | Methods**

### **2.1 | Approach**

To answer our research questions, we first carried out a systematic review to retrieve all published scientific literature on adaptive introgression and respective bibliographic meta-data. Then, we adopted a series of bibliometric analyses to understand the taxonomic coverage, geographic patterns, and temporal evolution of the retrieved literature. Additionally, we used salience analysis grounded on citation indices and attention scores, to understand the popularity level of the different studies among the scientific community and the public. Finally, we analysed the prevalence, polarity and relevance of adaptive introgression based on the perceptions from the authors of those studies, as well as the sentiment of the public towards this body of knowledge.

### **2.2 | Systematic review**

Following standard PRISMA systematic review protocols (Moher et al. 2009, O'Dea et al. 2021, Page *et al.* 2020), we carried out a systematic literature search for studies that explored the adaptive and evolutionary potential of natural introgression. We used ISI Web of Knowledge, Scopus, Google and Google Scholar, as the main search engines (Falagas et al. 2008). We used a combination of search terms relating to natural hybridization, genome, introgression and adaptation, avoiding the ones related to domestication and exotic/invasive species, with the aim of restricting the search only to natural phenomena of genomic introgression with potential adaptive outcomes, excluding all processes under direct or indirect human interference (breeding manipulations, genetic manipulation, invasive species scenarios, etc.). The selection of keywords was based on a review of previous keywords from a list of reference papers, and under a participatory approach with a team of scientists specialised in evolutionary processes. The final list of keywords included the most common and unambiguous words to reach the largest number of publications on the subject (see search details in supplemental materials for the full list of keywords). The timespan of our search was 1900-2019. Searches were carried out in November 2019 and were restricted to English.

Our initial search yielded 820 documents. After removing duplicates from the dataset, we excluded non-original studies, theoretical essays, opinion pieces, non-peer-reviewed papers, off-topic documents and non-indexed papers. Then we checked their reference list to search for other publications that included the terms under study (i.e. snow-ball effect). Finally, after excluding all reviews and book chapters, we screened the title and abstract of the remaining 436 articles individually to evaluate their eligibility for the analysis, namely: 1) if the papers complied with the natural origin for the adaptive introgression process and 2) if adaptive introgression was pointed by the authors as the main explanation for the biological processes under study. The final dataset included 358 relevant studies (webfigure 1; Supplemental materials). All papers were analysed in full only by the first author.

We extracted bibliographic information from the 358 studies. Each study was then reviewed to extract information on authors' initial perception about introgression and the temporal epoch and spatial location of the introgression phenomena reported in the study. We noted information on the taxa undergoing the introgression process. Finally, we reviewed which main method was considered in the publication, including the type of experiment, the type of introgression markers and whether whole-genome sequencing was performed or not. Detailed information about the variables extracted is available in table S1.

## **2.3 | Bibliometric analysis**

### *Geographic and taxonomic patterns in the published literature*

To investigate the associations between the geographical origin of researchers, the location of their case studies and the targeted taxonomic group, we used a spatial bipartite association network built using the GeoLayout 0.9.2.2. plugin from Gephi (<https://gephi.org/>) (scale of 20.000). We identified the main regions of origin of the introgression scientific study and the most important case studies based on their node weight (number of papers). Based on the betweenness centrality metric, we placed particular

attention on nodes representing case studies that were studied by several teams. This approach measures the influence of a case study over the flow of the scientific information used to find the ones that serve as a bridge between research teams (Ulrik and Faster, 2001).

### *Temporal changes in publication, methods and research areas*

Temporal changes in the number of published papers were tested through General Linear Models (GLM) with temporal series projections (until 2030) by the Expert Modeler Methods available on IBM SPSS Statistics software (v. 22; SPSS Inc, Chicago, IL). This approach was complemented with a linear regression, assessed through the coefficient of determination, between the number of published papers and time as a function of the methods used and research areas. We defined as the tipping point the temporal moment when the exponential trend lines ceased to show a reduced slope (Maroco, 2010).

## **2.4 | Salience analysis**

We searched in June 2020 each paper title in Altmetric Explorer, the web-based platform available through Altmetric.com which allows to browse and report the attention data that each paper has been receiving through online media (others include mainstream media mentions, peer reviews and citations to research in policy documents) (Tahamtan and Bornmann, 2020). Data included citations count and Altmetric Attention Score (AAS) (global and in context) recorded for each one of the 358 papers included in the review, including their geographical breakdown and temporal trends (Tahamtan and Bornmann, 2020). To determine the scientific relevance currently attributed to adaptive introgression, measured from the attention it is given, first we examined if paper AAS correlate with citation count (a traditional bibliometric indicator for research systems) (Okubo 1997) using Spearman correlation analysis. We then analysed AAS and compared: 1) all papers published in the same year and journal, 2) all papers published in the same year, 3) all papers published in the same journal and 4) all research outputs scored by Altmetric.com (28,900,000 outputs).

## **2.5 | Sentiment analysis**

### *Perceptions of scientists*

We obtained the data on the perceptions of scientists directly from the systematic review, namely the scientific area of the study, the authors' polarity opinion about adaptive introgression and the arguments used to justify it. We performed a Multi-Dimensional Scaling (MDS) tripartite network analysis with Gephi ThirdParties Plugins v. 0.9.2, to quantify the extent of known connections between these variables. The final layout represents the distance between nodes based on the similarities of their attributes, namely their connections' weight and connected nodes' identity. We chose the network metrics "node weight", "edges weight" and "node degree" to describe the main characteristics of the perception network (Algorithmics Group, 2009). Node weight, symbolised by node size, represents the total number of papers from each scientific area with similar authors' perception about adaptive introgression. Edge weight, symbolised by edge thickness, represents the total number of papers on which a connected pattern between two opinion characteristics simultaneously occurs. Node degree measures the number of

relationships between nodes. Nodes with high degree have many connections, suggesting that they may possess strong supporting arguments. All metrics were obtained directly from Gephi platform (Algorithmics Group, 2009).

We performed a temporal analysis of authors' perceptions of natural adaptive introgression in relation to changes in the amount of scientific evidence over time. We applied a distributed-lag model that is a dynamic model in which the effect of an x on y regression occurs over time, and not all at once. This modelling framework is useful to analyse variable associations in time series data even if data are non-linear and/or with delayed effects (DLNMs-distributed lag non-linear models) (Gasparrini, 2011). This approach is based on 'cross-basis', defined by a bi-dimensional space of functions that describe simultaneously the temporal relationship across the space of a predictor and the delay of its occurrence (Gasparrini, 2011). Thus, DLNMs analysis relies on a combination of these two sets of functions specifying the relationship between the dimensions of the number of scientific evidence and time lags, allowing to establish an immediate or delayed cause and effect relationship in the response variable (e.g. authors' prevalence perception – from "Very rare" to "Ubiquitous"). All DLNM analyses were executed in the *dlnm* R package (Gasparrini, 2011).

### *Public perceptions*

We considered the target public as a group of people broader than the scientific community, who show their interest in adaptive introgression through citation, reference, opinion and/or comment. We analysed 11,650 mentions by the public of the 358 adaptive introgression papers. The mentions, over multiple websites and different online platforms were mainly downloaded from Altmetric.com. Regarding twitter's mentions (from the social media network Twitter), the data exported from Altmetric.com only included the tweet's ID for an individual tweet. We obtained access to Twitter's Developer Portal, and taking this information into a Twitter API, we got access to each message. Finally, we used Postman software (<https://www.postman.com/>) to get the link from Twitter API and the Power BI Desktop software (<https://powerbi.microsoft.com/>) to get the final published tweets table of each adaptive introgression paper. Our approach complies with the Terms of Use and Developer Policy of the platform. All information extracted was anonymous or treated as confidential in respect to the General Data Protection Regulation (GDPR) from EU Regulation 2016/679. To perform the sentiment analysis based on lexicons, we uploaded each paper's mentions table into the *syuzhet* R package (Jockers, 2015). This package measures polarity (Positive, Negative or Neutral) and identifies eight different emotions, when present, for each message. It follows the basic emotion theory proposed by Plutchik (Plutchik, 1962): Anger, Anticipation, Disgust, Joy, Fear, Sadness, Surprise and Trust.

We standardized the differences between Positive and Negative mentions of each paper using the following formula:

$$stPP = \frac{Pos - Neg}{TotalMentions}$$

Where:

“stPP” represents the Standardized Polarity Perception,

“Pos” represents the total number of positive mentions,

“Neg” represents the total number of positive mentions,

“TotalMentions” represents the total mentions obtained by an individual paper.

We then performed a temporal analysis of public polarity perception (stPP) of adaptive introgression as a function of temporal changes in the number of scientific evidence of its occurrence through DLNMs analysis. Lastly, we followed the same approach to analyse the temporal changes in public emotions that adaptive introgression studies raise in public opinion as a function of temporal changes in the amount of scientific evidence for its occurrence.

Finally, to understand whether public opinion and the emotions that a scientific paper about adaptive introgression elicits are conditioned by the taxonomic group under study, we established the relationship between global polarity perceptions and public emotions for each taxonomic group under study. To illustrate this relationship, a chord diagram was produced using the Circlize R package (Gu, et al. 2014). This diagram was complemented with a linear regression, assessed through the coefficient of determination, between the standardized polarity perception of the public and scientists for each taxonomic group under study in each paper as a function of the phylogenetic distance from humans (Maroco, 2010).

## 3 | Results

### 3.1 | The scope and evolution of knowledge about adaptive introgression

Our systematic review showed that adaptive introgression studies were mainly carried out by researchers from North America (>50%) (Especially USA – with 167 published works) and Europe (>30%), with the remaining regions showing very few research teams working on adaptive introgression (figure S1). The scientific knowledge covered case studies from multiple geographic areas: North America (28% of all case studies), Europe (19%), Africa (12%), Asia (9%), South America (8%), Central America (7%), Oceania (4%), Eurasia (4%), global (3%), Pacific Ocean (2%), Atlantic Ocean (1%) and Indian Ocean (1%) (figure 1a).

The spatial bipartite association network showed a geographical proximity between case studies and research teams of 56.7%, meaning that most studies were performed by teams from the same geographical region (figure 1a, table S2). There was also a strong association between the taxa studied and the geographic origin of the research teams (figure S2). In North America, plants represented almost

half of all studies (48%), especially angiosperms (38%). In Central and South America, invertebrates were the most represented taxa (43% and 48%, respectively), followed by birds (24%) and angiosperms (26%). Similarly, in Africa invertebrates represented 58% of all studies, followed by fish (21%). In Europe, like in North America, angiosperms were the most represented taxa (33%), but most studies focused on animals (63%). In Asia, mammals (36%), followed by fish (22%), were the most represented taxa, whereas in Oceania and Pacific islands all taxa had similar representation (angiosperms: 20%, birds: 20%, mammals: 16%, reptiles: 12% and insects: 12%) (figure S2).

Globally, adaptive introgression has been demonstrated in a wide range of taxa since Bacteria (1%), Protists (<1%), Fungi (3%) and Plants (27%) until Animals (69%). Mammals were the most studied taxonomic groups with 34% of all studies, followed by angiosperms (84% of plant studies) and insects (27% of all animals). Yeast represented 67% of studies of adaptive introgression in Fungi.

### *Temporal evolution of the adaptive introgression literature*

We observed only a few studies published during the 20th century, with the highest prevalence in the 1990s, which saw an increase in published evidence for adaptive introgression, particularly from botanical controlled experimental studies involving the use of quantitative trait locus (QTL). A slight increase in the number of publications between 2000 and 2012 was observed alongside the rising of Methodological developments from the Human Genome project (<https://www.genome.gov/>).

The increased publication rate from 2012 was accompanied by a methodological revolution due to the generalization of genomic approaches, mainly through the advent of high throughput sequencing (HTS) and the use of Whole-Genome Sequencing and Single Nucleotide Polymorphisms (SNPs). These techniques proved to be effective in detecting cost-efficient way genomic areas under introgression and their adaptive value. Increasing in an exponential way through time (GLM\_SNPs [family="poisson"]:  $R^2=0.80$ ,  $p<0.05$ , GLM\_Whole-Genome [family="poisson"]:  $R^2=0.76$ ,  $p<0.05$ ), these techniques also contributed significantly to an exponential growth of adaptive introgression knowledge, which is evident by the cumulative number of published papers over time (GLM\_Total Number of Papers [family="poisson"]:  $R^2=0.94$ ,  $p<0.05$ ) (figure 1b).

This growth pattern was evident in the different scientific fields (Anthropology, Phylogeny/Genealogy, Plant Sciences, etc.), and particularly in Evolutionary Biology. Bioinformatics was also identified as an emerging important field that became prevalent since 2016 (figure 1c) (Pfeifer and Kapan, 2019).

The genomic revolution in adaptive introgression studies began in 2012, when the annual average of published papers increased from  $1.9 \pm 3.1$  (1966-2011) to  $34.5 \pm 10.1$  (2012-2019), equating to an average annual increase of 1824.14% of papers ( $X^2_1 = 97.37$ ,  $p<0.01$ ). Temporal series projections, following the current publication growth rates, demonstrated an annual publication rate reaching 130 papers/year in 2030 (95% CI: 100-155) (figure S3).

## **3.2 | Perceptions of scientists**

Our results showed that 12 different scientific areas have been exploring adaptive introgression. The authors of 78% of the studies (N=280 papers) presented a scientifically grounded opinion about this topic. The argument polarity results show that the great majority of the authors had a positive opinion on adaptive introgression (node weight = 164). These results are mainly supported by authors' perceptions about the positivity of the impact of introgression on species' "adaptation to changing/new environmental conditions" (edges' weight = 143), a result influenced by studies in the scientific areas of Plant Sciences (edges' weight = 51) and Anthropology (edges' weight = 30). However, most of the studies were carried out in Evolutionary Biology (node weight = 140), where authors presented the greatest number of biological arguments to support the sense of the polarity of their opinions (node degree = 45), which were mainly positive (edges' weight = 67) (figure 2a). Negative arguments were derived mainly from Evolutionary Biology (edges' weight = 9.0), Plant Sciences (edges' weight = 6.0) and Anthropology (edges' weight = 4.0). The main negative argument presented is that introgression may "act against speciation" (figure 2a).

The total number of positive and negative arguments was similar (N = 24 and N = 20, respectively) even though in the total number of mentions, the latter were significantly lower (N = 296 and N = 78, respectively). Authors who presented mixed arguments (positive and negative) tended to use the greatest number of biological arguments (node degree = 56, betweenness = 1113.37) (figure 2a).

Analysing the interest of the scientific community in the topic, we found a strong relationship between Altmetric.com scores and the traditional citation metrics (GLM [family="poisson"]:  $R^2=0.72$ ,  $p<0.05$ ) (figure S4). The position of adaptive introgression papers in relation to the Altmetric.com score when analysed in comparison with all papers published in the same year, in the same journal, in both simultaneously and, especially, when analysed in relation to all published literature, revealed a bimodal distribution (figure 2b). Although some studies have received little attention, a quarter of the papers were within the top 5% of the most cited and commented papers globally.

There was no clear relationship between the temporal increase in the number of papers providing evidence for adaptive introgression and authors' prevailing perception (GLM [family="Gaussian"]:  $R^2=0.04$ , NS) (figure S5). The overall cumulative exposure–response relationships based on DMNL models revealed a slightly positive impact of the amount of evidence on author's perception about the prevalence of adaptive introgression (DLMN:  $R^2=0.08$ , NS) from "unknown" (0) to "few cases" (1) after a rate of 20 paper/year (95% CI: infrequent [-1] – common [2]) (figure S6).

### **3.3 | Public perception and sentiment**

A total of 14,214 mentions were recorded between 2000 and 2019 (including shares). Of these, 11,650 mentions were of adaptive introgression papers expressing some kind of opinion (polarity, emotions or both). The source of the vast majority of mentions was Social Media (N=11,628) followed by News and Blogs (N= 2,193) from traditional on-line newspapers. Academic sources were infrequently mentioned (N=145). Policy and Patents documents showed limited interest in the topic (N=24).

The overall cumulative exposure–response relationships, summing up the contributions for the 20 years of lag considered in the analysis, showed a tendency for scientific publications to have just a slightly positive impact on public opinion of adaptive introgression with polarity perception reaching 0.1 after a rate of 20 papers/year (95% CI: - 0.2 – 0.2) (figure 3b). However, this impact does not seem to be immediate and presents a reversal of trend (from negative to positive) approximately following a delay of 7 years (figure 3c). A temporal analysis showed that the increase in the amount of evidence for adaptive introgression has nearly no immediate impact on public polarity perception (figure 3a). It occurs with a delay that promotes a high positive effect of scientific publications on the positivity of public opinion, increasing exponentially with high number of papers. However, there is almost no effect on public opinion from a reduced number of annually published papers, even after considering the delay (figure 3).

The publication of a large number of scientific papers had an immediate emotional public response (both negative and positive). After that, people's emotions began to immediately and exponentially diminish over time (figures S7, S8, S9 and S10). Of the 9,867 mentions recorded that expressed some kind of emotions, with positive emotions being more frequent than negative ones (especially trust (N=1958 mentions), followed by anticipation (N=1,581 mentions) and surprise (N=1,314 mention). Anger (N=825 mentions) was the least evoked emotion by the papers. In contrast, fear (N=1,111 mentions) and disgust (N = 960 mentions) were the most often expressed negative emotions (figure 4b).

This disparity between positive and negative emotions explained the greater number of mentions by expressing a global positive polarity about adaptive introgression (N=4,179 mentions). However, often the interest in the topic was not accompanied by a clear position on the orientation of the opinion, so neutral mentions were slightly higher than positive mentions (N=4,440 mentions, figure 4b). On the other hand, there was a disparity in the attention given by the public when comparing the mentions about papers on vertebrates (N=8,850 mentions - including Humans - the majority of mentions [N=4,654]) with all the other taxonomic groups (figure 4b).

The distribution of mentions by the different emotions and directions of polarity that the papers raise in the public followed the same pattern as their total number (more positive than negative) (figure 4b). However, in all taxonomic groups and in the global studies about adaptive introgression, scientists held more positive opinions about adaptive introgression than the general public ( $F_{(1, 10)} = 54.260, p < 0.05$ ) (figure 4a). Finally, contrary to what happens within the scientific community (GLM [family="poisson"]:  $R^2 = 0.13, NS$ ), the polarity of public opinion (although always positive) has a positive correlation with the phylogenetic distance from modern human beings (GLM [family="poisson"]:  $R^2 = 0.86, p < 0.05$ ). In other words, the more distant from humans the phenomenon occurs, the more people consider adaptive introgression to be positive (figure 4a).

## 4 | Discussion

## 4.1 | Scope and evolution of knowledge about adaptive introgression

The geographical scope of taxa under study is widespread, despite a slight tendency for geographical proximity between case studies and research teams. This shows that there have been no major geographical biases in adaptive introgression studies. Scientific interest in adaptive introgression has been increasing over the past two decades. However, since 2012 the number of papers published per year began to increase exponentially. This turning point marks the beginning of the genomic revolution in adaptive introgression studies. Most likely, it occurred in response to the increased use of whole genome sequencing and reduced representation genome sequencing methods, such as restriction-site associated sequencing (RADseq), and the development of new high throughput sequencing platforms and the subsequent reduction in sequencing costs (Hayden, 2014). The cost per sequenced genome was dropped from US \$3 billion to less than US \$1,000 from 2000 to 2012 (Hayden, 2014). These methodological and sequencing advances have enabled the scientific community to compare the genomes of a large number of individuals, thus increasing the probability of identifying shared genomic regions under selection (Kuhlwilm et al. 2019, Ryan et al. 2018). Our temporal series models predicted that this trend will continue through the next decade (figure S3, Supplemental material) in response to the growing interest in the topic and the widespread use and development of these genomic analysis tools and sequencing platforms.

## 4.2 | What do we think about adaptive introgression?

Adaptive introgression has received considerable attention from both the scientific community and the public, with high average rankings compared to the total current scientific literature. Several papers ranked within the top 5% most cited and commented papers globally.

Despite the exponential increase in scientific evidence since 2012, the genomic revolution does not seem to have changed authors' perception of the prevalence of adaptive introgression in nature, being frequently underestimated with authors citing difficulties in demonstrating its presence (Reid et al. 2012). In terms of polarity in the opinions of the scientific community about adaptive introgression, the total number of positive and negative arguments is rather balanced. However, positive arguments are clearly most mentioned among scientists. Authors' perception of whether the impact of introgression on species was positive is mainly based on potentially beneficial outcomes for "species adaptation to changing/new environmental conditions" (Acosta and Premoli, 2018, Boratynski et al. 2014, Hamilton et al. 2013, Lewontin and Birch, 1966, Melo-Ferreira et al. 2014). The main negative argument put forward by scientists is that adaptive introgression may have negative impacts because it "acts against speciation" (Naisbit et al. 2003, Payseur et al. 2004).

The source of public opinion about adaptive introgression studies was dominated by social media (and mainly Twitter), followed at great distance by traditional on-line newspapers. Academic media sources and policy documents infrequently refer to adaptive introgression papers, showing limited interest in the

topic. This seems to indicate that there is a much greater interest among the general public in the subject than the importance given to it by traditional media and institutions both in terms of dissemination and socio-political orientations.

The increased number of papers providing scientific evidence for adaptive introgression led to marked increase in positive public opinion, however, only following a seven year delay. There was either no initial response or even an initial negative impact on people's perception. Empirical literature refers to the difficulties of investigating research phases impacting on society (Trochim, 2010). On some occasions, delay of scientific translation should be necessary to ensure the accuracy and efficacy of new evidence or advances (Morris et al. 2011). However, it is relatively accepted by both the scientific community and policy that quick translation of research into practice is somehow positive (Morris et al. 2011). Nevertheless, the research translation process is known to undergo long periods of time-lag (Kilbourne et al. 2020, Morris et al. 2011).

Our results demonstrate that only the annual publication of a sufficiently large number of papers providing evidence for adaptive introgression influences public perception of its merits and consequently of genetic miscegenation. This trend of increase in positive opinions is probably to accentuate in the future if the number of publications on the topic will continue to increase exponentially up to at least 2030, as we have predicted.

For all taxonomic groups, and overall in studies of adaptive introgression, there is a significant disparity between the opinions of scientists and the general public, whereby scientists hold more positive opinions. This disparity between the opinions of scientists and the public follows the trend of other studies on public perception about scientifically controversial topics, such as the origin of climate change and the risks of nuclear power (Taylor et al. 2014).

There is a taxonomic bias revealed by the great disparity in the attention given by the public to papers on vertebrates (mainly on humans) compared to all other taxonomic groups (Troudet et al. 2017). Regardless, papers referring to all taxonomic groups frequently receive positive opinions from the public, mostly eliciting positive emotions (primarily anticipation and trust). The polarity of public opinion (although always positive) positively relates to the phylogenetic distance from human beings, whereby the more distant the taxa are from humans, the more people consider adaptive introgression as positive. This pattern can be explained by different degrees of bias in the perception about genetic miscegenation according to taxonomy once societal inclinations strongly correlate with taxonomic bias (Troudet et al. 2017). Groups phylogenetically closer to human beings are the target of greater attention and importance whereas they are simultaneously the target of higher degrees of prejudice (Troudet et al. 2017). Bias has the potential to inappropriately influence the scientific process (Fanelli et al. 2017) because "scientists are human beings rooted in cultural contexts" (Gould, 1978). However, the scientific method usually shield scientists from the consequences of their own cultural biases (Lewis et al. 2011).

## **4.3 | Public sentiment in response to evidence of adaptive introgression**

Scientific work in psychology has pointed to the relevance of emotions in addition to cognition in public perception and decision-making (Kahneman, 2011, Stanovich and West, 2008a). The publication of a large amount of scientific evidence for adaptive introgression has an immediate increasing effect on the emotional public response (both negative and positive). People's emotions rise immediately and diminish exponentially over time, showing an intense, but temporary, emotional cascade. The first reaction responds to an intuitive mode of thought that is fast, involves limited judgement, and is driven by emotions. It is later replaced by an analytical mode of thought (based on evidence), which is more rational, slower, involving more effort and deliberate reasoning (Kahneman and Frederick, 2002). This replacement over time can help explain the increase in positive polarity in the medium-long term. Time-lag helps to clarify this change in the mode of thought, from instinctive to analytical (Whitmarsh, 2011), once emotion based reactions decrease over time (Taylor et al. 2014).

The overall cumulative exposure–response relationships of all sentiments expressed by public mentions about adaptive introgression papers, summing up the contributions for the 20 years of lag considered and analysing their balance with the increase of scientific evidence published over time, show just a slightly positive impact on the expression of all positive emotions (mainly anticipation and joy). According to the probabilistic sequence of events involved in the development of an emotion, anticipation responds to stimulus events like "novelty" promoting the behaviour of examining and the effect of exploration whereas joy explains the pride of achievement (Izard, 2007). This means that the increase in evidence outweighs the potential negative effect of time on people's positive emotional response, allowing them to experience the urge to learn more about the benefits of genetic miscegenation and taking from there the pride of discovery.

However, the same trend happened for two negative emotions (disgust and fear). Disgust is a response to a "gruesome object" and promotes rejection whereas fear explains flight for safety in response to an "obstacle" and stimulates destructive feelings (Izard, 2007). Despite occurring to a lesser extent compared to positive emotions, paradoxically, the increase in evidence, by offsetting the negative effect of time, raises a slight increase in some people in the identification of genetic miscegenation as being susceptible to repugnance. It stimulates looking at it as an obstacle to their safety and boosting reactions of rejection and destructive opinions.

In contrast, the increasing number of papers over time influences negatively public emotions of sadness and anger. Sadness responds to stimulus events like a "life-changing loss" promoting the effect of reintegration, whereas anger explains the frustration in response to blocked goals (Izard, 2007). In both cases, the increase in evidence complements the effect of time in decreasing such reactions to genetic miscegenation.

The individual proximity to the facts under evaluation, derived from personal experience or shared by mimicry, conditions the emotions that are expressed. For example, social groups that have experienced the effects of extreme weather events (e.g. wildfires or severe droughts) tend to experience higher levels of anger, sadness and fear when confronted with climate change issues (Loureiro and Alló, 2020). In

contrast, groups that have never been confronted with the consequences of nuclear accidents tend to have higher levels of trust in nuclear energy (Loureiro and Alló, 2020).

On the other hand, studies show that ignorance is at the root of stereotypes and prejudice (Matusitz, 2012) and that these influence negative emotions like disgust and fear (Dasgupta et al. 2009), which can only be countered by high degree of communication (Matusitz, 2012, Nshom and Croucher, 2017). However, the emotions also vary according to the signal of potential threat. For example, disgust increases bias against homosexuality, but anger did not. Instead, anger increased bias against ethnic minorities (e.g. Arabs) in western societies, but disgust did not (Dasgupta et al. 2009). In this context, genetic miscegenation is more susceptible to prejudice derived from disgust than anger.

Overall, public interest in adaptive introgression leads to an immediate rise of different emotional reactions that increase with increasing number of scientific evidence on the topic. Immediately after that emotional response, a cascade of divergent opinions spreads by emotional contagion and mimicry among social groups (Ferrara and Yang, 2015, Sonnby-Borgström et al. 2003) due to different social norms and circumstances of the common identities they share within (Pagel, 2012). However, negative emotions are potentially oversized because reactions to negative news tend to be stronger (Soroka et al. 2019).

## 4.4 | Caveats and limitations

The impact of scientific developments on society is often difficult to measure mainly because data on perception of scientific facts are hard to obtain and work with. Using algorithms like those employed by Altmetric.com, it is possible to compile and organise all information available online about a set of papers retrieved from a systematic search of a scientific subject. When analysing such a large amount of data, the relevance of subjectivity decreases when the intention is to find general trends. Still, even approaches designed to mimic and replace the human brain still have important limitations. In sentiment analysis, for example, there are still limitations in the interpretation of forms of literary expression, such as irony or sarcasm (Sykora et al. 2020). However, recent studies showed that the percentage of sarcastic and ironic content in social media is normally very low (Sykora et al. 2020). In traditional media and official documents their use should be even lower. So, in large datasets, sarcasm, irony and even the use of humour may be much less of a concern than was previously thought (Puschmann and Powell, 2018). Given that these expressions are probably rare in the dataset covered in our study, this is unlikely to influence the results of the general trends.

We assume that written mentions are behaviours that reflect the opinions or attitudes of the writer. Yet, opinion is usually associated with a certain degree of subjective judgment (Sacks and Gary, 2012). On the other hand, the subjectivity of individual judgment is also subject to conflicts with social norms, political and cultural contexts (Dange, 2016). In other words, we could see a change in social behaviour (such as the proportional increase in positive mentions about adaptive introgression) due to a potential change in social norms (e.g. greater tolerance or acceptance/appreciation of genetic miscegenation) derived from the increase in the number of scientific evidence, but it may still not mean that beliefs and/or mentalities

are in fact being changed (Schultz et al. 2007). Therefore, it seems probably that the publication of a large amount of scientific evidence in the medium-long term has promoted a change in opinion polarity about adaptive introgression and consequently about genetic miscegenation after undergoing an initial emotional response and a certain degree of rejection. However, whether this can promote an effective change in people's mentality and beliefs will require further studies.

## 4.5 | Conclusions

We show that the genomic revolution provided mounting evidence for adaptive introgression, which is mainly understood by the scientific community as particularly beneficial for species ability to adapt to changing or new environmental conditions. Scientific evidence suggests that adaptive introgression, or even genetic miscegenation, from a scientific point of view, represents a key natural evolutionary process. The exponential increase in scientific evidence for the beneficial effects of genetic miscegenation led to more positive public perception of the topic in the medium-long term. Therefore, we argue that continuing the development of knowledge on adaptive introgression will allow Evolutionary Biology to scientifically refute eugenics and other evolutionary theories that promote taxa 'purity'. In the past, these ideas were employed to justify racism and other forms of discrimination. However, in light of current scientific evidence, only bias in perception appears to stand in the way of accepting the fundamental role that genetic miscegenation plays for life.

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## Figures

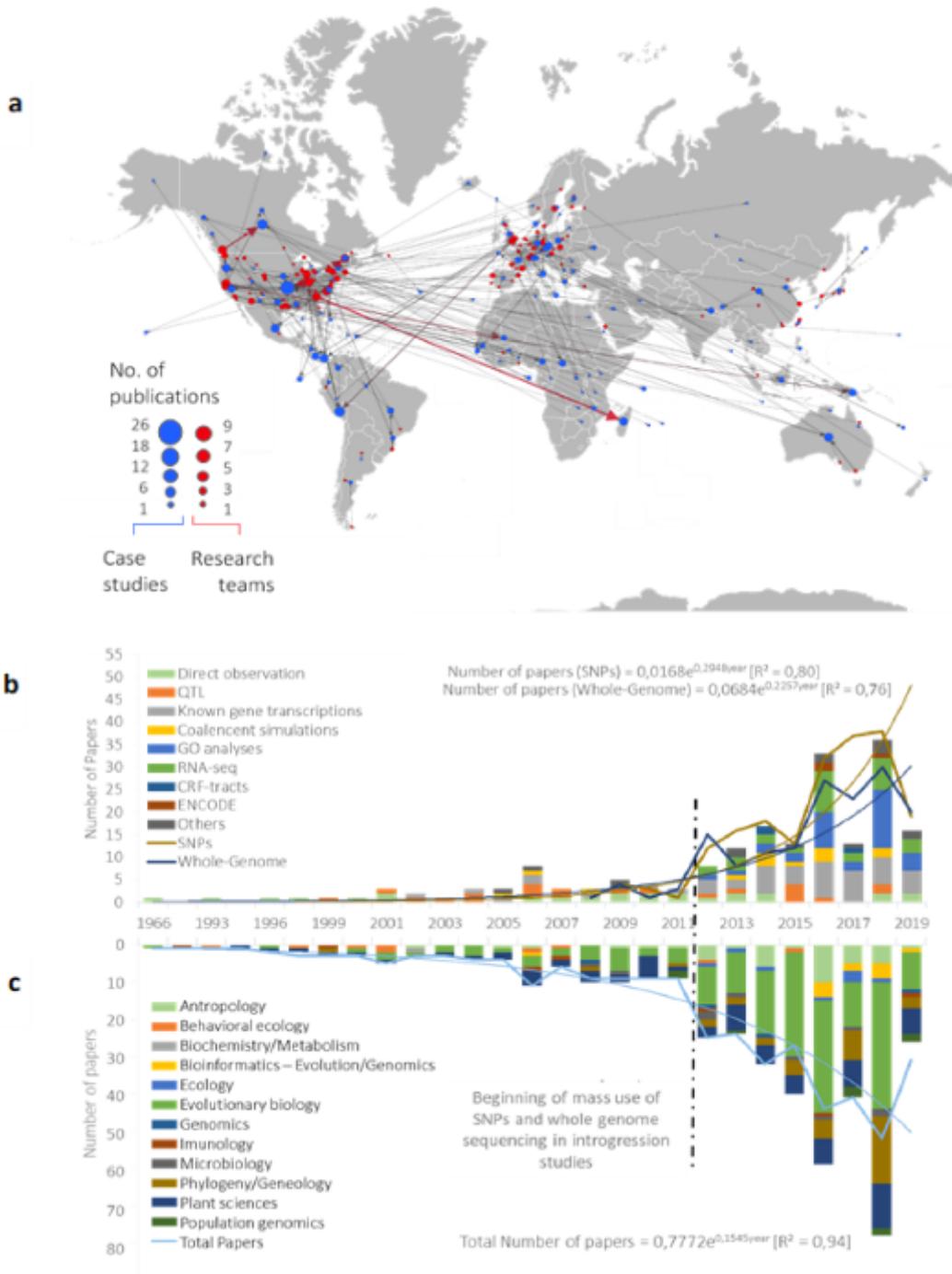
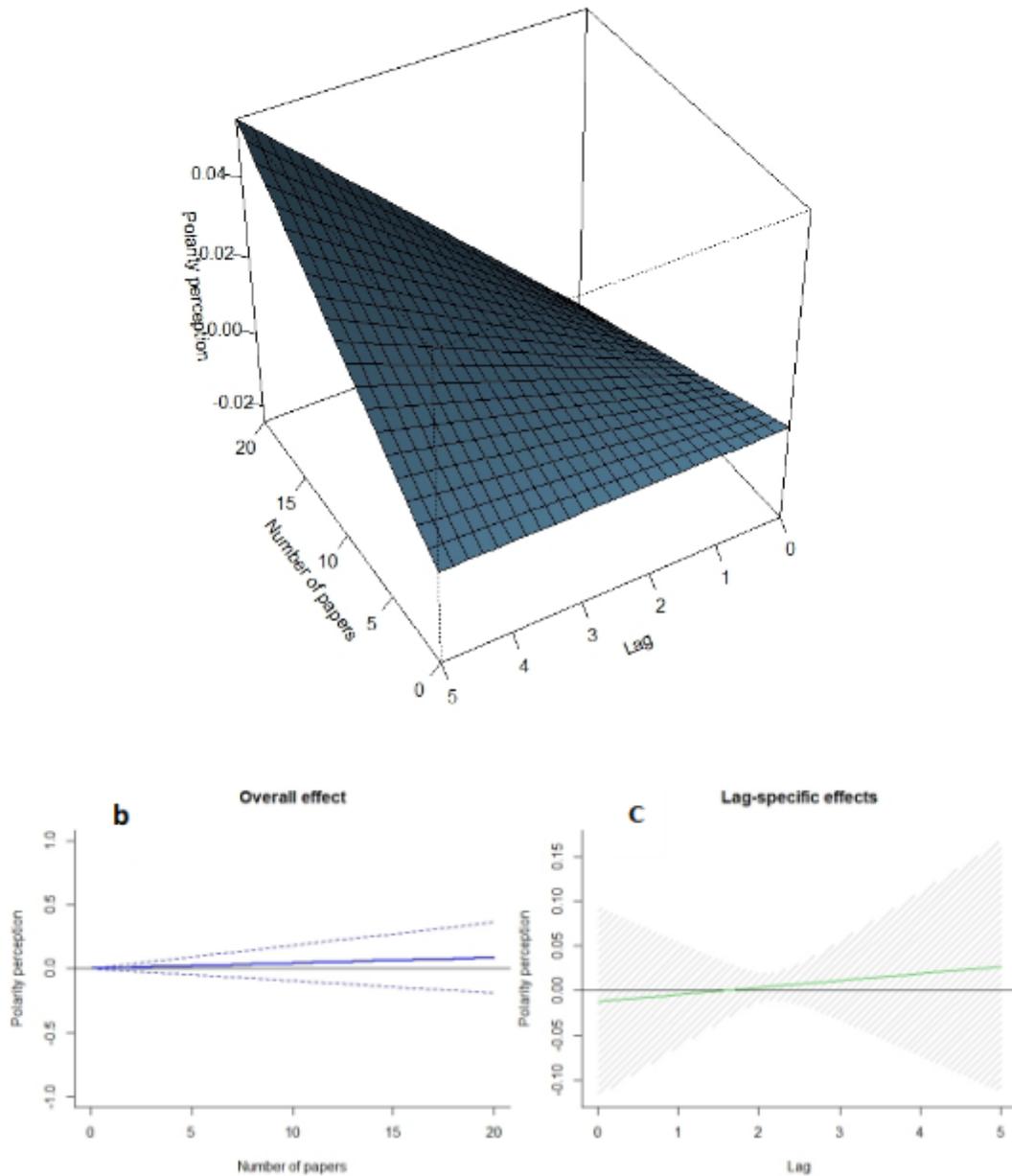


Figure 1

Spatial networks of case studies featured in the meta-analysis (blue dots) performed by each research team with a specific host geographic location (red dots) (a). Case study locations were georeferenced based on the description of the study area provided within each paper. Circle sizes reflect the number of papers from a specific location. Arrows represent directional pathways from the team to the case study with line width representing the number of papers published by each team on the specific case study. Temporal changes in the number of published papers on adaptive introgression by methodology (b) and scientific field (c). The solid lines represent the correlation between the number of papers and time and the dashed line shows the tipping point, when the trend line started to show an exponential increase – representing the beginning of the genomic revolution in adaptive introgression studies.



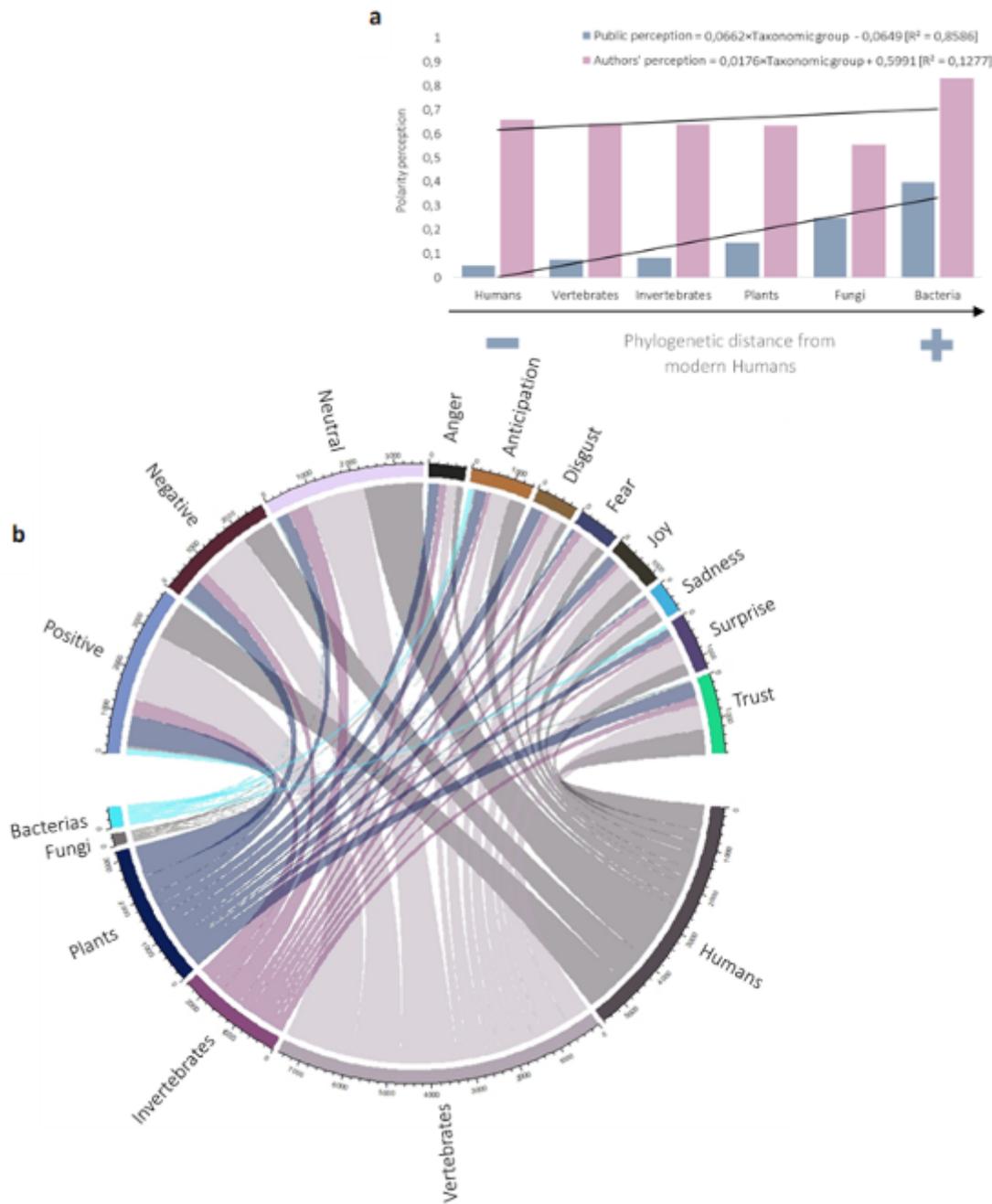
is represented between 0 (first position) to 100 (last position). Within them white solid lines boxplots include medians (horizontal white line) and average (white dot), boxes indicate quartiles and ranges, simultaneously.



**Figure 3**

Three-dimensional plot showing temporal changes (2000 to 2019) of the estimated exposure–lag–response association between the number of papers providing evidence for adaptive introgression and the standardized polarity perception by the public (stPP), with the average as reference and each Lag period corresponding to 4 years (a). Overall cumulative exposure–response relationships between the temporal changes (2000 to 2019) of the number of papers providing evidence for adaptive introgression and standardized polarity perception by the public (stPP), predicted from the model with no interaction

(interpreted as the average), with 95% CI (b). Lag–response relationships between the number of papers providing evidence for adaptive introgression and stPP, with 95% CI and each Lag period corresponding to 4 years (c).



**Figure 4**

Standardized Polarity Perception (stPP) correlation with taxonomic groups under study (a). Grey and pink bars represent public and authors' perception, respectively. Solid lines depict the relationship between their stPP and the different taxonomic groups under study based on the phylogenetic distance from modern Humans. Hierarchical network chord diagram with expanded endpoints illustrating public total polarity perception and expressed emotions about adaptive introgression papers from different taxonomic groups under study (b).

## Supplementary Files

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