Selection against domestication alleles in introduced rabbit populations

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ABSTRACT

Humans have moved domestic animals around the globe for thousands of years. These have occasionally established feral populations in nature, often with devastating ecological consequences. To understand how natural selection shapes re-adaptation into the wild, we investigated one of the most successful colonizers in history, the European rabbit. By sequencing the genomes of 297 rabbits across three continents, we show that introduced populations exhibit a mixed wild-domestic ancestry. We show that alleles that increased in frequency during domestication were preferentially selected against in novel natural environments. Interestingly, causative mutations for common domestication traits sometimes segregate at considerable frequencies if associated with less drastic phenotypes (e.g., coat color dilution), while mutations that are likely strongly maladaptive in nature are absent. While natural selection largely targeted different genomic regions in each introduced population, some of the strongest signals of parallelism overlap genes associated with neuronal or brain function. This limited parallelism is likely explained by extensive standing genetic variation resulting from domestication together with the complex mixed ancestry of introduced populations. Our findings shed light on the selective and molecular mechanisms that enable domestic animals to re-adapt to the wild and provide important insights for the mitigation and management of invasive populations.

Keywords: feralization, domestication, natural selection, artificial selection, biological invasions, behavior, invasive species

INTRODUCTION

When domesticated species adapt to an anthropogenic environment, long-term selective pressures associated with fitness in the wild are relaxed and novel selective pressures arise. This process over thousands of years led to the evolution of a common set of phenotypes favored by humans (*e.g.*, tameness and fancy coat colors) that otherwise would be subjected to strong negative selection in wild populations (1-3). Conversely, when domesticated animals move outside the sphere of human influence and recolonize natural settings, they become re-exposed to many of the former selective pressures, as well as novel ones. Over time, these populations thrive and frequently reverse to the original phenotypes that characterize their wild ancestors through a process known as feralization (4-6 and references therein). Understanding the molecular mechanisms by which feralization operates can thus provide valuable insights about how populations establish in new environments and, ultimately, about the process of evolution.

The European rabbit (*Oryctolagus cuniculus*) is one of the most successful colonizer animal species. From a circumscribed native distribution in the Iberian Peninsula and France, rabbits are now widespread in all continents, except Antarctica, and in over 800 islands around the globe (7), thriving in various ecological contexts and considered an invasive species in many regions (8, 9). This cosmopolitan distribution is the result of a series of human-mediated introductions in the last 1,000 years (7, 10-14). Rabbit domestication predates this expansion, and it is believed to have occurred in France between AD 500 and 1000 (15-18). Since most of the species' expansion occurred after its domestication, many populations were formed by the release of domestic rabbits (7). While in some instances, these domestic importations failed to establish until wild rabbits, better adapted to the natural environment, were introduced (19), in others, domestic rabbits were able to adapt, thrive, and eventually establish feral populations that still exist today (7). The numerous introductions of rabbits worldwide offer a powerful and replicated study system to elucidate the molecular mechanisms associated with feralization.

The process of animal domestication is thought to result from shifts in allele frequency of many loci across the genome (20). This highly polygenic architecture is well illustrated by genomic studies of wild and domestic rabbits (18). For example, out of ~50 million single nucleotide polymorphisms across the genome, only 20 variants were found to be fixed for alternative alleles between wild rabbits from the native range, from which domestic rabbits were derived, and domestic rabbits (18). Since the ancestral "wild" alleles still segregate in domestic rabbits for most loci, even if at low frequency, these loci have the potential to revert to the ancestral state (21) when exposed to a natural environment. This source of readily available standing genetic variation could potentially provide the means to explain the rapid evolutionary change and phenotypic reversal that frequently occurs when domesticated animals are released back into the wild. While the origin and

role of alleles involved in the process of domestication have been widely studied, the fate of these alleles in natural environments, and their subsequent role in adaptation outside captivity, is not well understood.

In this study, we leveraged the worldwide colonization of the European rabbit to investigate the genetic changes induced by feralization. Using whole genome sequencing of 297 individuals, we compared levels and patterns of genetic diversity between six introduced rabbit populations against domestic rabbits and wild rabbits from the native range. We show that introduced rabbit populations are characterized by a mixture of wild and domestic ancestry and that alleles that have increased in frequency during domestication are enriched among those that underwent strong shifts in frequency in introduced populations. Our results highlight the complexity of animal introductions and show how natural selection can reshape the variation of domestic animals when exposed to natural environments, providing a general view of the molecular mechanisms enabling their adaptation to the wild.

RESULTS

Colonization bottlenecks in introduced rabbit populations

We generated low-pass whole-genome sequencing data from six introduced rabbit populations across three continents (Fig. 1A). In South America, Neuquén and Tierra del Fuego; in Europe, Skåne and Gotland; and in Oceania, Australia and New Zealand. All these introductions have occurred in the last 200 years and historical records suggest they were largely independent (*SI Appendix*, Supplementary text). We additionally generated whole-genome sequencing data for wild rabbits from the native range (Iberia and southern France) and domestic individuals from seven breeds that are representative of the phenotypic diversity seen in domestic rabbits. In total, we resequenced 297 individuals at an average sequencing coverage of 1.5X (Supplementary Table 1), taking advantage of approaches based on the estimation of genotype likelihoods to calculate population genetics statistics. These approaches have become increasingly common in recent years in population genomics, as they provide a cost-effective and accurate estimation of allele frequencies while bypassing the need for genotype calling (22).

We began by investigating patterns of population structure with a principal component analysis (PCA, Fig. 1B). Overall, the populations were well differentiated across the two main axes of variation (MANOVA, Wilk's $\Lambda = 5.85 \times 10^{-3}$, $F_{14,576} = 496.9$, $P < 1.0 \times 10^{-15}$, partial $\eta^2 = 0.988$). Along the main axis (PC1, explaining 34.0% of the total variation), wild and domestic rabbits showed high differentiation and were placed on opposite sides of the distribution. The introduced populations were distributed between the two groups along this putative domestic-wild axis, except for Tierra del Fuego which clusters at the far end of domestic rabbits. The second principal component (PC2, explaining 20.3% of the total variation) separates the individuals from Neuquén and Gotland from the remaining samples. An analysis of ancestry using an admixture algorithm based on genotype likelihoods (Fig. 1C, Extended Data Fig.1) was broadly consistent with the PCA results. At $K = 2$, the two ancestry components separate the domestic and Tierra del Fuego populations from the remaining dataset and at $K = 4$, the populations of Neuquén and Gotland emerged as differentiated from the remaining groups. Increasing values of K resolved the expected substructure associated with each population.

We then estimated genome-wide levels of nucleotide diversity for each population (Fig. 1D). As expected, diversity in all introduced populations was lower than that in the native range populations. This could be explained by a combination of bottlenecks (due to a limited number of founders) and domestic ancestry because domestic rabbits have significantly lower nucleotide diversity than their wild ancestors (17, 23). The genetic diversity of the populations that were placed in the extremes of the PCA plot (*i.e.,* Neuquén, Tierra del Fuego and Gotland) was similar to

that in domestic breeds (π domestic = 0.45%). This is likely a consequence of strong bottlenecks and could explain their clustering position in the PCA analysis.

Mitochondrial DNA (mtDNA) analysis corroborates the patterns described above: haplotypic diversity in populations from the native range was markedly higher than that in introduced populations (Extended Data Fig.2). The mtDNA phylogeny also illustrates the variation and complexity of the colonization history of the different populations (Fig. 1E, Extended Data Fig.3). For example, some populations contain haplotypes distributed across the phylogeny (Neuquén, Australia and New Zealand), while others show a tight clustering consistent with a strong colonization bottleneck (Gotland and Tierra del Fuego). Samples from geographically close locations are not substantially more likely to cluster in related haplogroups, further underlining that these introductions were largely independent and did not follow a simple step-wise colonization pattern. Despite this diversity, all mtDNA haplotypes belong to the *O. c. cuniculus* subspecies, the European rabbit lineage that is found in Northeastern Iberia and France, and which was the direct source of domestic rabbits (17). Although some reports indicate a Spanish origin for some introduced rabbit populations (12), which would increase the probability of a direct contribution by the subspecies from the Southwestern Iberia (*O. c. algirus*), we did not find evidence of this in any population.

High levels of domestic ancestry in introduced rabbits

To estimate the contribution of domestic ancestry to each introduced population, we next estimated an ancestry index that enabled us to assess the relative contributions of wild and domestic genotypes for each individual based on a set of autosomal variants that are informative for domestic/wild ancestry (n = 1,995). Corroborating the previous analyses, this index suggests that most introduced populations have a predominantly domestic ancestry, albeit mixed with wild (Fig. 2A). The relative proportion of wild and domestic ancestry was very similar among individuals within each population, and the average domestic contribution for each population varied between 47.5% (Skåne) and 80.8% (Tierra del Fuego; Supplementary Table 2) We note, however, that selection against domestic alleles (see below) could lead to a reduction of the inferred domestic ancestry when compared to the true proportion of neutral admixture background.

To further evaluate the contribution of domestic ancestry to the introduced populations, we calculated an outgroup f_3 statistic, which measures shared drift between pairs of populations in relation to an outgroup (24). We applied the statistic to trios with wild rabbits as the outgroup, and domestic rabbits and each introduced population as ingroup. Divergence was higher between domestic and wild rabbits from the native range, with intermediate values for each introduced

population. There is a very strong agreement with the ancestry index analysis above in terms of the relative differences among populations (Fig. 2B). For example, rabbits from Tierra del Fuego showed the largest divergence from the wild outgroup and Skåne the least. These results are consistent with a scenario of mixed wild-domestic ancestry for all introduced rabbit populations, regardless of their geographic context. However, the degree of admixture, the specific affinities between populations, and the overall levels of nucleotide diversity reflect each population's colonization history.

Selection against domestic alleles

The population from Tierra del Fuego exhibits a predominantly domestic ancestry (Fig. 2). This provides an opportunity to study the effects of natural selection on variants that were initially selected during domestication but subsequently exposed to selective pressures commonly found in the wild. We tested the prediction that the adaptation to natural environments could be facilitated by standing genetic variation present in domestic rabbits, since the domestication process is not associated with significant allele fixation (18). We calculated allele frequency differences (ΔAF) for each autosomal variant between i) domestic rabbits and rabbits from the native range, and ii) between domestic rabbits and rabbits from Tierra del Fuego (Fig. 3A). To specifically test whether selection against domestication alleles is more frequent than expected by chance, we defined lowly and highly differentiated variants as those with $\Delta AF < 0.75$ and $\Delta AF \geq 0.75$, respectively. Highly differentiated variants between wild and domestic rabbits are expected to be enriched in loci selected during domestication, while highly differentiated variants between domestic rabbits and rabbits from Tierra del Fuego should be enriched in loci associated with adaptation to the wild following the introduction to Tierra del Fuego.

For positions with lower ΔAF between rabbits from the native range and domestic rabbits ($\Delta AF < 0.75$, n = 16,276,491), 0.73% were highly differentiated between domestic rabbits and Tierra del Fuego ($\Delta AF \geq 0.75$, n = 118,296). Strikingly, when considering positions with higher ΔAF between wild and domestic rabbits ($\Delta AF \geq 0.75$, n = 53,235), the proportion that was also highly differentiated in the Tierra del Fuego versus domestic rabbits was 3.79% ($\Delta AF \geq 0.75$, n = 2,019). This suggests that domestication alleles are over five times more likely to revert to a high frequency of the wild-type allele than other loci (one-sided Fisher's exact test, $P < 1.0 \times 10^{-15}$, odds-ratio = 5.385). While imposing an artificial threshold to define highly differentiated variants may risk inducing over-interpretation of these results, a closer inspection further suggests that this enrichment is increasingly stronger for variants that are highly differentiated between domestic and native populations (Fig. 3B). This can be interpreted as variants that shifted more strongly in allele

frequency during domestication were also more strongly selected against when reintroduced to a natural environment.

We next investigated the genome-wide distribution of these 2,019 variants with simultaneous high ΔAF in the two contrasts. Their distribution in the genome was not uniform but instead enriched in specific regions (Fig. 3C). By summarizing the number of these variants in overlapping 100 kb windows, we identified 398 windows with five or more of these variants that defined 71 independent genomic regions, which overlapped 171 protein-coding genes. We examined the top five regions. The 1st top outlier region overlapped the gene *PHACTR4* (159 variants). PHACTR4 is a phosphatase and actin regulator that is required for neural tube and optic fissure closure, and enteric neural crest cell migration, which has been linked to abnormal retina morphology, exencephaly and educational attainment (25,26). The 2nd region was located near an uncharacterized gene that is a likely homologue of *RPL35A* (62 variants), which has been connected with bone marrow failure and anemia (27). Other top five regions also overlapped or were in the vicinity of genes associated with brain function or neurogenesis. These are *KLF4* (53 variants), which has been implicated in neurogenesis (28, 29) and previously shown to have been a strong target of selection during rabbit domestication (18); and *DPP10* (46 variants), which encodes an auxiliary subunit of voltage-gated potassium ion channels that are integral to signal processing in neuronal cells (30, 31). The fifth region (43 variants) contained genes that might be associated with other relevant phenotypic traits that might have undergone relaxed selection following domestication, such as immune response (*CD180/MAST4*, 32).

The fate of domestic variants of known phenotypic impact

Rabbit domestication has produced a variety of phenotypes for which the underlying causal genes and/or variants have been identified (33-41). Following up on the finding that domestication alleles are disproportionally more likely to be the targets of selection during feralization, we assessed the frequency of occurrence in each population of domestic mutations known to be associated with specific phenotypes. We focused on ten mutations associated with variation in coat color, fur texture and length, morphology and fat coloration (Fig. 4). All these mutations can be found in rabbits of different breeds but are unlikely to be detected by our previous analysis focused on variants that differentiate all domestic rabbits from wild rabbits from the native range.

Five mutations were completely absent in any introduced population. These were linked to either coat structure and length (rex and angora), changes in pigmentation (black, and black/tan) or drastic morphological changes (dwarf). Four other mutations linked to coat color variation were present in the majority of the introduced populations at low-to-moderate frequencies, with the

highest prevalence being the dilute mutation of *MLPH* that was present in 10 out of 30 individuals sampled from Gotland. The *BCO2* variant causing yellow fat was also relatively common (7.4% to 13.3% in three populations). We did not detect any of these domestic alleles in wild rabbits from the native range. These results support the hypothesis that there is a strong variation in selective pressures associated with mutations of domestic origin..

Population-specific selection against domestic ancestry

Next, we investigated the distribution of genomic regions that are more strongly differentiated between each of the introduced populations and domestic rabbits. These regions should be enriched for loci where domestic ancestry was likely selected against when compared to the admixed genetic background of both wild and domestic origin found in all introduced populations. To accomplish this, we calculated ΔAF using a sliding-window approach (n = 81,842 windows, Extended Data Fig.4) and then combined the results using a modification of the *di* statistic (42). This scan revealed multiple genomic locations as strong outliers when compared to the genome-wide average (Fig. 5A). The top 0.1% windows from the autosomal distribution were located on 27 independent genomic regions containing 52 protein-coding genes, 14 of which (26%) were already outliers in the previous analysis in Tierra del Fuego rabbits (see above). These regions of high differentiation show signatures of selective sweeps: these top 0.1% ΔAF windows in each population (Extended Data Fig.4) show a significant enrichment for lower values of Tajima's *D* when compared to genome-wide values (Welch's *t*-test, $P < 4.7\times10^{-4}$, in all six populations; Extended Data Fig.5, Supplementary Table 3).

The strongest cross-population signal of differentiation between domestic rabbits and the introduced populations overlapped the Yes-associated protein 1 gene (*YAP1*; chr1:114,550,000-114,725,000), with four windows that were in the top 1% of the empirical distribution in each of the six contrasts (Fig. 5B, Extended Data Fig.4). Among several organismal functions, *YAP1* activity is necessary for neural stem cell differentiation into neural progenitor cells (43-45); knock-down of *YAP1* expression in rat hippocampal neurons lead to impaired dendrite development (46). The 2nd top outlier overlapped *RSPH4A*, which encodes for a component of the radial spoke head of cilia (47). Several of the other top five outlier windows overlapped or were in the vicinity of genes that can be associated with brain function. *CPQ* encodes a carboxypeptidase that interacts with thyroglobulin to release thyroxin (48, 49), the levels of which are regulated by environment-induced stress (50); *MIB1* encodes a ubiquitin ligase that controls neurogenesis and gliogenesis in the spinal cord and has been implicated in synaptic plasticity and memory formation in the hippocampus (51, 52). The fifth region contains *PRKG2*, which encodes a serine/threonine protein kinase that is

highly expressed in the brain where it plays a role in circadian rhythm regulation and anxiety-like behavior (53-55). This gene could also be associated with other phenotypes relevant to the re-adaptation to the wild since it has been implicated in bone growth and linked to several abnormal morphological phenotypes in mice, such as abnormal bone ossification, small bones and disproportionate limbs and cranium (56).

We next assessed the degree of parallelism among the six introduced populations. We calculated ΔAF for each pair of domestic vs. introduced population for 20,483 non-overlapping windows of 100 kb, and intersected the top 1% (Fig. 5C). We found that the great majority of these top windows (n = 755; 78.9%) were specific to one population and 202 (21.1%) were outliers shared by two or more populations. Only one window was shared among the six and contained the *YAP1* gene (Fig. 5B). The observed overlap was generally higher than expected by chance (Bonferroni-corrected $P < 0.05$; Supplementary Table 4). For example, the null expectation of 1% outlier sharing between two populations is approximately two windows, while in our dataset, we found that this number ranged from 10-to-45 windows. For comparisons involving three or more populations, the expectation of overlap was below one, but we still observed multiple shared outlier windows in almost all intersections. Taken together, these results suggest a significant but modest degree of parallelism, with the great majority of regions being population-specific outliers.

DISCUSSION

Understanding the causes that determine the success of a population in a novel environment is a question whose implications intersect a wide range of fields, from conservation to evolutionary biology. The repeated introduction of domesticated organisms into natural environments provides a unique framework for understanding how this process unfolds. Taking advantage of the unique history of rabbit colonization and the replication provided by the numerous translocation events in a variety of geographic and ecological contexts, we used whole-genome resequencing of 297 rabbits across three continents to understand the molecular mechanisms by which domestic animals re-adapt to the wild and establish feral populations.

A striking observation in our data is that all studied populations are characterized by a blend of wild and domestic genotypes. This mixed ancestry suggests that most successfully introduced rabbit populations originate either from multiple introductions of different stocks or from importations of already mixed stocks. The pervasiveness of wild ancestry is surprising as domestic rabbits were easier to acquire and transport and were available at the time when all the colonization events studied here occurred. One potential explanation for this pattern is that the spread of rabbits could have followed a stepping-stone model where an admixed stock of animals was moved from place to place; however, historical records for the populations we analyzed suggest that, with exception of Australia and New Zealand, they originate from independent introductions (*SI Appendix*, Supplementary text). This is corroborated by our analyses, which indicate an important degree of genetic distinctiveness. A more likely explanation could be associated with the fitness advantage that wild ancestry provides. In Australia, a large body of historical records report that multiple domestic introductions failed to become established until an introduction of rabbits with wild ancestry triggered a biological invasion that swept the entire continent (19). This signature of "exoferality" in rabbits (in contrast to "endoferality", when introduced populations derive from an essentially domestic ancestor) has been found in other introduced plants and animal species (5, 57), and could be argued as a key factor promoting the establishment and persistence of human-mediated introductions. We note that the majority of recorded instances of rabbit introductions have been on small oceanic islands (7), where selective pressures are typically relaxed, particularly those linked to predation, competition for resources, and plant chemical defenses (58, 59). This is well illustrated by the Japanese island of Ōkunoshima, also known as the "Rabbit Island", where a large population of tamed rabbits, segregating for a wide range of colors and other domestic-like traits, has thrived for over 50 years (60). However, most of the introduced populations from our study thrive in continental environments populated by predators and where competition for resources with other species is presumably stronger. In more competitive and predator-rich environments, domestic alleles are more likely to be deleterious, so mixed wild-

domestic ancestries are in turn more likely to establish successful populations than introductions based strictly on domestic rabbits.

If domestication traits presumably prevent population establishment, two questions remain: how do populations with a predominantly domestic origin adapt to a wild environment, and what happens to the fraction of the genome associated with domestic ancestry in the mixed populations during this process? Our results suggest that an important way to mitigate the deleterious impact of domestication variants during adaptation to the wild is negative selection against these alleles. In rabbits from Tierra del Fuego, a population of predominant domestic ancestry, we found a genome-wide signature of stronger selection against alleles that have more strongly increased in frequency during domestication. Domestication in rabbits acted mostly on standing genetic variation that was pre-existing in ancestral wild rabbits (18), with some notable exceptions such as large effect alleles that were cherry-picked by breeders. As a consequence, most variants contributing to rabbit domestication have not become fixed in domestic breeds, which promotes the conditions for wild-type alleles to rise in frequency if natural selection becomes again a predominant factor. This pattern was stronger near genes with functions likely to be associated with traits relevant for domestication, in particular brain function, raising the intriguing possibility that some of these signatures could be important to compensate for the reduced fear and flight response that characterizes domestic rabbits and are highly deleterious in natural settings. The fate of domesticated alleles in wild settings is perhaps more directly demonstrated by our analysis focused on causative mutations known for controlling several fancy traits, such as coat color and fur-type. Interestingly, some of the mutations underlying less extreme coat color phenotypes (*e.g.*, dilution) or the coloration of fat were present at moderate/high frequencies, likely because they are not strongly deleterious in some natural habitats and therefore tolerated. Domestic variants that are linked to phenotypes with more pronounced phenotypic effects are often absent, suggesting that they were likely purged by selection. Although these results can be confounded by the specific domestic ancestry for each introduced population (some alleles could have been already rare or absent in the source population, particularly for breeds like rex and angora), many of these variants are both common across domesticated rabbits and have a recessive mode of inheritance, which increases the chances of them being introduced into a population undetected. Combined, these factors are likely contributing to the atavism commonly observed in feral populations.

The several instances of adaptation to wild environments in introduced rabbit populations could potentially result from parallel genetic changes. One striking example of a locus shared by the six introduced populations overlaps the *YAP1* gene, which has a known role in neural cell development. Nevertheless, the vast majority of putative signatures of selection were not shared across populations. This is a good illustration of the power of standing genetic variation at multiple

loci to drive fast adaptation through soft selective sweeps (61). This highly polygenic and independent pattern of selection is, however, also linked to a genetic legacy of mixed wild and domestic ancestries in introduced rabbits, since all our populations had a significant contribution of wild ancestry (~19-53%, depending on the population). These results thus add important insights to the growing body of knowledge that has been collected in other species with feral populations. For example, selective sweeps in feral chickens in Hawaii targeted mostly loci not associated with domestication itself (62). In dingoes, a mixed scenario of reversions to functional wild-type alleles in some loci and a rise in frequency of domestication alleles seems to have occurred in a context of local adaptation (63). This is also the pattern observed in free-living Soay sheep, in which coat color alleles at several loci were either under positive or negative selection, depending on specific fitness components (64). Our study expands on these previous studies, which were mostly focused on single populations, by investigating multiple iterations of the adaptation process.

Feralization has often been seen as a simple process of re-adaptation to the wild from a previously domesticated population (sometimes called de-domestication, but see 4, 5, 65). This simplistic view is challenged by our empirical data on multiple introduced populations, as well as previous studies in other species, that illustrate the complex roles of admixture, local environment, and demography in shaping how re-adaptation to the wild occurs. For example, our introduced populations have adapted to strikingly different habitats, so readaptation to the wild occurs in tandem with local adaptation to novel environments that differ from those in the native range (see also 66, 67). Feralization in rabbits is thus not a simple reversal of domestication (5). Moreover, the timing and frequency of admixture between wild, domestic, and feral populations can potentially have a profound impact to shape the available genetic variation (64, 68), highlighting the crucial roles that the initial genetic composition and standing genetic variation play in the successful establishment of introduced populations.

Across the world, domestic species play a major role in human activity. When these species run wild, however, they can cause devastating economic consequences. Extensive damage to native fauna and flora can lead to irreversible impacts on natural ecosystems. Our study demonstrates how these domestic species can circumvent the limitations imposed by the domestication process and successfully adapt to novel locations. These findings therefore contribute to a better understanding of the feralization process and have the potential to inform conservation policies.

METHODS

Sampling and whole-genome resequencing

We collected 297 samples from domestic rabbits, wild rabbits from the native range, and wild rabbits from multiple introduced populations (Fig. 1B, 1C, Supplementary Table 1). For wild rabbits from the native range (*Oryctolagus cuniculus cuniculus*), we collected a total of 49 samples from several localities: Caumont (n = 8, France), La Roque (n = 10, France), Villemolaque (n = 10, France), Tarragona (n = 11, Spain) and Zaragoza (n = 10, Spain). From domestic rabbits, we collected a total of 62 samples from seven breeds: Belgian hare (n = 10), Champagne d'argent (n = 10), Dutch (n = 9), English silver (n = 3), Flemish giant (n = 10), French lop (n = 10), and New Zealand white (n = 10). For the introduced populations, we focused on the following six populations: Neuquén (n = 42), Tierra del Fuego (n = 27), Skåne (n = 30), Gotland (n = 30,), Australia (n = 27) and New Zealand (n = 30).

DNA was isolated from blood or ear tissue using a commercial membrane-based kit (Easyspin, Citomed, catalogue no. SP-DT-05). The quantity and integrity of DNA were assessed using a NanoDrop instrument, Qubit dsDNA BR Assay Kit (Invitrogen, catalogue no. Q32853), and through agarose gel visualization. Individual Illumina sequencing libraries were then produced using a Tn5-based tagmentation protocol with PCR amplification based on (69) (more details in 70, 71). Following library preparation, libraries were pooled in equimolar concentrations and sequenced on an Illumina instrument (2x150 bp) at an average coverage of 1.5X (Supplementary Table 1). Whole-genome sequencing data are available in the Sequence Read Archive under BioProject PRJNA936804.

Read mapping, variant calling and allele frequency estimation

Read quality was evaluated using *FastQC* v0.11.8 (https://www.bioinformatics.babraham.ac.uk/projects/fastqc/). Reads were then mapped to the rabbit reference genome assembly (OryCun2.0, 18) using *BWA-MEM* (72) with default settings and duplicates were removed using *PICARD* v2.0.1 (http://broadinstitute.github.io/picard/). Mapping statistics were calculated using *SAMtools* (73) and custom scripts.

ANGSD v0.929 (74) was used to calculate population-specific allele frequencies (-doMaf 3) based on genotype likelihoods, imposing for each position a minimum mapping quality of 30 (-minMapQ 30), minimum base quality of 20 (-minQ 30), a minimum of 10 individuals with data (-minInd 10), and setting the reference base as the major allele (-doMajorMinor 4). Since *ANGSD* provides little control over the variant quality filters, variant calling was further carried out using the haplotype-based variant caller *Freebayes* v1.0.0 (75), using the flags -H, -J and -g. To avoid calling variants overlapping repetitive elements or copy number variants, positions with coverage

above 1500 were skipped. Reads with a mapping quality lower than 30 and base reads with a quality lower than 20 were not considered. Prior to the analysis, we further applied several stringent filtering steps to our catalog of variants using *vcftools* v0.1.16 (76) and the *vcffilter* tool of *vcflib* v1.0.2 (77). First, we kept only biallelic markers. Second, we excluded variants with a quality score below 300 ("--minQ 300" in *vcftools*). Finally, using *vcffilter* we filtered variants based on: i) allele balance ("AB > 0.25 & AB < 0.75 | AB < 0.01"), ii) discrepancy in the properly paired status of reads supporting reference or alternate alleles "PAIRED > 0.05 & PAIREDR > 0.05 & PAIREDR / PAIRED < 1.75 & PAIREDR / PAIRED > 0.25 | PAIRED < 0.05 & PAIREDR < 0.05", and iii) alleles that are only seen on one strand ("SAF > 0 & SAR > 0 & RPR > 1 & RPL > 1"). Compound variants were decomposed into single variants using the program *decompose* using *vt* (78). For each of the variants passing filters, we obtained allele frequencies by intersecting the list of variants with the list produced by *ANGSD* using *BEDTools* v2.26.0 (79).

Population structure

To evaluate population structure, we conducted a principal component analysis (PCA) on genotype likelihoods using *PCAngsd* with default parameters (80). We restricted the analysis to those positions called with *Freebayes* and passing quality filters. The resulting covariance matrix was used to estimate principal components and individual loadings with the function *prcomp* from *R* v3.6.3 (81). Differences between populations were tested with a MANOVA (statistical significance considered at $P < 0.05$) on rank-transformed PC1 and PC2 values (minimal deviations from normality within-groups were observed following quantile-quantile plot inspection), using *PAST* v4.08 (82). Effect sizes (partial η^2) were calculated with a custom *R* script. The same genotype likelihoods used for the PCA were used as the input for *NGSadmix* (83) to calculate individual admixture proportions. We filtered triallelic positions, positions with base quality below 30, reads with mapping quality below 30, secondary and duplicate reads, reads with multiple best hits, and reads with one or both of the mates not mapping correctly. The analysis was run for several values of K (2 to 10), imposing a minor allele frequency of 0.05.

Nucleotide diversity

ANGSD was used to estimate levels and patterns of genetic variation in our populations. We first generated a maximum likelihood estimate of the unfolded site frequency spectrum and used this to calculate nucleotide diversity (π, 84) in 100 kb non-overlapping windows. Nucleotide diversity estimates were obtained by dividing the value obtained for each window by the total number of sites passing filters (we excluded windows that did not have at least 50,000 sites passing filters).

Mitochondrial DNA diversity

To extract mitochondrial DNA (mtDNA) read information from the individual whole-genome sequencing data, we started by creating a novel reference genome based on the OryCun2.0 assembly to reduce the probability of true mtDNA reads erroneously mapping either to nuclear mitochondrial DNA (NUMTs) or to smaller unplaced scaffolds that could have resulted from the misassembly of mitochondrial reads. For this, we used *BLASTN* v2.11.0 (85) to align the annotated mitochondrial scaffold of OryCun2.0 to the rest of the genome, and hard-masked all hits apart from the mitochondrial scaffold itself. The WGS data were then re-mapped to this new hard-masked reference (using *BWA MEM* and default parameters) and *SAMtools* was used to extract reads that aligned exclusively to the mitochondrial scaffold.

From these alignments in *bam* format, *fasta* files were generated using *HTSBOX pileup* (https://github.com/lh3/htsbox), using a majority-allele rule. Only reads with a mapping quality of 30 and bases with a quality of 30 were kept. After these filters, sites were classified as missing data if they had a read depth of 4× or less. The *fasta* format files were combined and converted into a nexus format file using *AliView* v1.26 (86). Median-joining haplotype networks for both the control region and the cytochrome b gene were built with *PopART* v1.7 (87). A Bayesian tree was inferred with *BEAST* v2.6.7 (88). The best-fitted mutation model (GTR) was determined by *ModelTest-NG* v0.1.6 (89, 90), under the Bayesian information criterion (BIC). The demographic model selected was the Coalescent Extended Bayesian Skyline with a strict clock. Both strict and relaxed clocks were tested and evaluated with a Bayes factor, no significant differences were found. Final analyses were run three times independently with 100,000,000 iterations. *Tracer* v1.7.2 (91) was used to assess convergence across runs. The first 10% of the samples of the Markov chain of runs were used as burn-in and the tree files were combined using *LOGCOMBINER* v2.6.7, included in the *BEAST* package. The final tree was generated with the *R* package: *ggtree* (92).

Ancestry index

To quantify the contribution of wild and domestic ancestry for each introduced population, we calculated a summary ancestry index based on nearly diagnostic alleles between wild rabbits from the native range and domestic rabbits. We first calculated the frequencies of the non-reference alleles to determine the number of SNPs with differences in allele frequency higher than 0.9 (excluding data from the X chromosome and unplaced scaffolds). We identified a total of 1,995 single nucleotide polymorphisms (SNP) meeting this criterion to form a reference panel of nearly diagnostic alleles maximizing ancestry differences between wild rabbits from the native range and domestic rabbits. To calculate individual ancestry scores, we summarized allele counts at the diagnostic positions using *SAMtools mpileup*, and then converted the *mpileup* file into the sync

format using *PoPoolation2* (93). Since the average depth of coverage across samples of 1.5X prevents calling individual genotypes, we randomly subsampled one base per individual at any given position and used this information to calculate the proportion of wild-like or domestic-like alleles in each individual. The calculation of the index from the diagnostic reference panel and sync file with allele counts was done using a custom script (available at: https://github.com/PJADPereira/hybridindex). When running the script, we performed 100 independent replicates (each time a different allele may be selected in samples with >1 read), setting a minimum distance between markers of 200 kb to account for close linkage between markers. The average number of wild-like and domestic-like alleles were calculated to obtain individual ancestry scores.

f_3 statistics

Outgroup f_3 statistics were calculated using *TreeMix* v1.13 (94). *TreeMix* uses population-level allele frequencies obtained from allele counts as inputs, which given our low-coverage dataset could provide biases if allele counts were directly used. To account for this, we used the single-read sampling option in *ANGSD* to randomly subsample one allele per individual at each SNP (scoring the alleles as reference or alternative), summing the number of alleles of each individual by population to generate the typical *TreeMix* input counts file. We then ran the *threepop* v0.1 subprogram, with 500 SNP per block for estimation of standard error. For each run, we constructed an input file with three populations: domestic, wild and each introduced population independently. For plotting, we considered the triplet (wild from native range, domestic, introduced population), in which wild native rabbits were considered the outgroup. Each autosome was run independently, and results were averaged.

Inspection of causal variants underlying common breeds

To verify the presence of alleles in introduced populations that are causal of (or strongly associated with) known domestic rabbit phenotypes, we compiled information from the literature on alleles of interest from the following phenotypes: angora (*FGF5*; 33); red, black, and brindle (*MC1R*; 34, 35); rex (*LIPH*; 36); dilute (*MLPH*; 37); yellow fat (*BCO2*; 38); dwarf (*HMGA2*; 39); black/tan (*ASIP*; 40); and albino (*TYR*; 41) For each of these mutations, we identified its coordinate in the OryCun2.0 assembly and gathered allele counts for each population at the respective locus (plus 1,000 bp around each side) using *SAMtools mpileup*. We restricted the analysis to reads with a base quality and mapping quality above 30. We then visually inspected the *mpileup* files to detect the presence of each allele in each individual of the dataset. For the large structural variants associated with black/tan and dwarf, we complemented this analysis by inspecting read depth with *SAMtools*

and visualizing alignments with *IGV* v2.16.2 (95). Due to the low coverage whole-genome resequencing that prevented us from obtaining individual genotypes, we therefore scored for each population the minimum number of individuals carrying at least one copy of the mutant allele.

Outlier sharing between populations

To identify the loci most strongly differentiated between domestic rabbits and introduced populations, we used the d_i statistic (42), which was originally conceived to investigate parallel divergence in dog breeds. Using the allele frequencies obtained previously, we calculated differences in allele frequency (ΔAF) between each introduced population and domestic rabbits, summarized the values across the genome in overlapping windows (100 kb with 25 kb overlap) and used these values to calculate d_iΔAF using the following formula for each window:

$$d_i\Delta AF = (\Delta AF_{domestic\text{-}populationA} - \text{average } \Delta AF_{domestic\text{-}populationA}) \,/\, \text{standard deviation } \Delta AF_{domestic\text{-}populationA}$$

To obtain the final value of d_iΔAF for each window, these values were then summed across all pairs of population-domestic comparison, and the top 0.1% and 1% outliers of the diΔAF distribution were considered for further inspection. To calculate Tajima's *D* (96) for each population across the genome (100 kb windows with 25 kb overlap), we used *ANGSD* (with the same approach used to calculate π), To test for signatures of selection in the top 0.1% outliers of the ΔAF scan of each population, we compared *D* values of those windows with genome-wide *D* values using a non-parametric Welch's *t*-test in *R* (*t.test* function with var.equal=FALSE; statistical significance considered at $P < 0.05$), and estimated effect sizes with Hedge's *g* (with a custom *R* script). To investigate if outlier overlap was significantly greater than expected by chance, we repeated the ΔAF analysis for all six domestic-introduced comparisons in non-overlapping 100 kb windows and extracted the top 1% windows of all six sets. Multi-set intersection testing was performed with the *R* package *SuperExactTest* (97) through the online shiny application (https://network.shinyapps.io/SuperExactTest/), considering a background population size of n = 20,483 (the total number of calculated windows when intersecting all contrasts). Statistical significance was considered at $P < 0.05$ after Bonferroni correction.

DATA AVAILABILITY

Whole-genome resequencing data are available in the Sequence Read Archive (www.ncbi.nlm.nih.gov/sra) under BioProject PRJNA936804.

CODE AVAILABILITY

A script developed for the calculation of the hybrid index is available at https://github.com/PJADPereira/hybridindex

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AUTHOR CONTRIBUTIONS STATEMENT

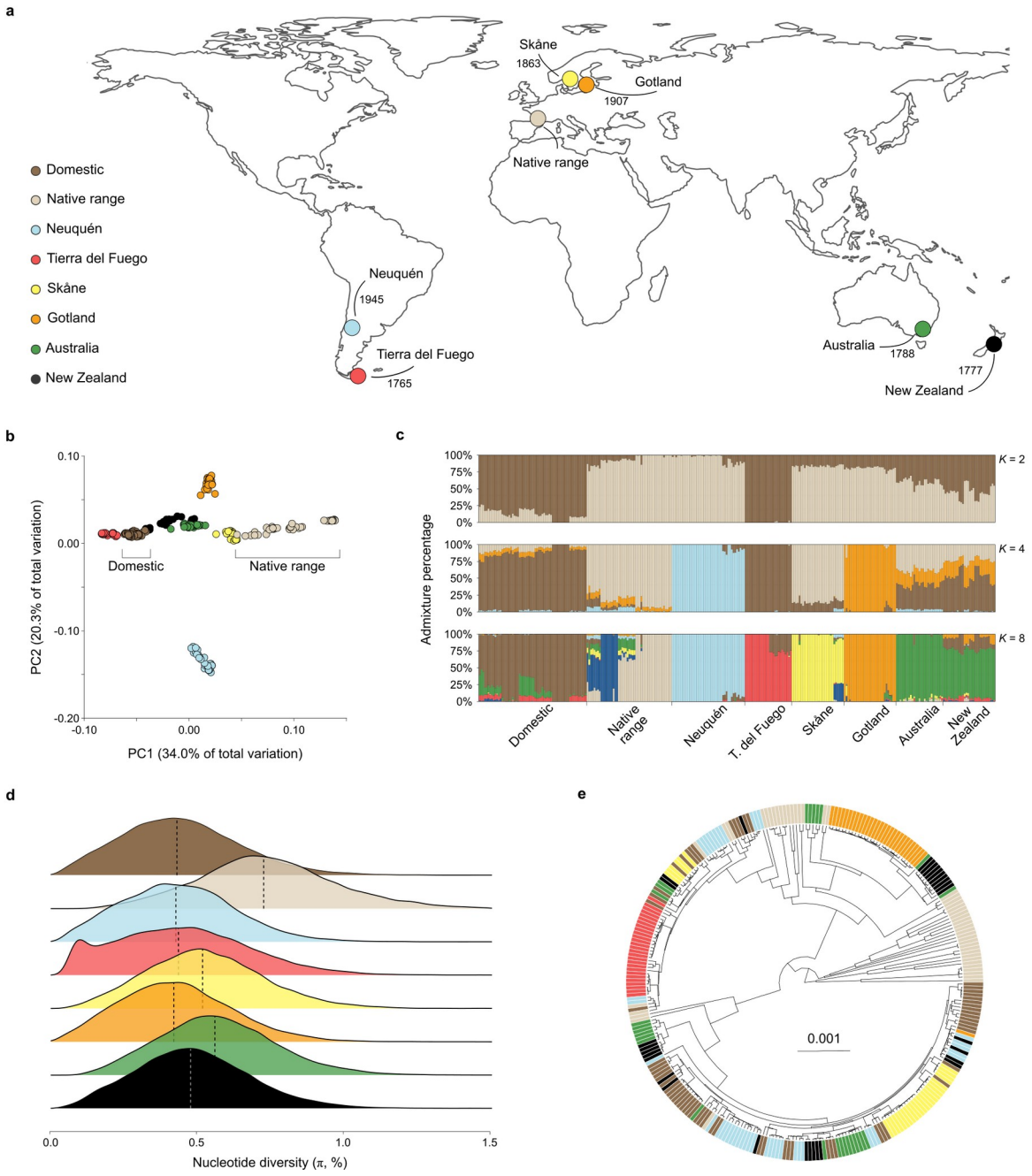
M.C., L.A., N.F., P.A. and J.M.A. conceived the study; N.B., J.A.D., H.G., M.L., T.S., C.-G.T., G.Q.,R.V. and N.F. coordinated and performed sample collection. C.G.S and S.A. performed experiments. P.A., M.C., J.M.A., P.P., C.-J.R., E.S., E.E., R.F., Y.Z., F.M.J. and L.A. analyzed data. P.A., J.M.A., L.A. and M.C. wrote the paper with input from all other authors.

COMPETING INTERESTS STATEMENT

The authors declare no competing interests.

608 **FIGURE LEGENDS**

609



611 **Fig. 1 | Population genomics of introduced rabbits across three continents. (A)** Introduced
612 rabbit populations were sampled across several localities on three different continents,
613 corresponding to six colonization events. Estimated dates for the earliest known introductions are
614 given (*SI Appendix*, Supplementary text). We also sampled multiple localities from the native range
615 (Iberia and France) and seven domestic breeds. Map obtained from www.naturalearthdata.com. **(B)**
616 Principal component analysis based on genotype likelihoods. The percentage of variance explained
617 by each component is given in parentheses. Individuals are colored according to their population of

origin. **(C)** Admixture proportions were calculated for a sample of domestic rabbits, wild rabbits from the native range and six introduced populations, calculated based on genotype likelihoods. Expanded results for a larger number of values of *K* are shown in Extended Data Fig.1. **(D)** Genome-wide estimates of nucleotide diversity (π, %) for each population, based on non-overlapping 100 kb windows. The dashed line in the middle of each density plot indicates the median of the distribution. **(E)** Bayesian tree of mtDNA sequences. Each individual is colored according to the population of origin. Support values (Bayesian posterior probabilities) for each node are shown in Extended Data Fig.3.

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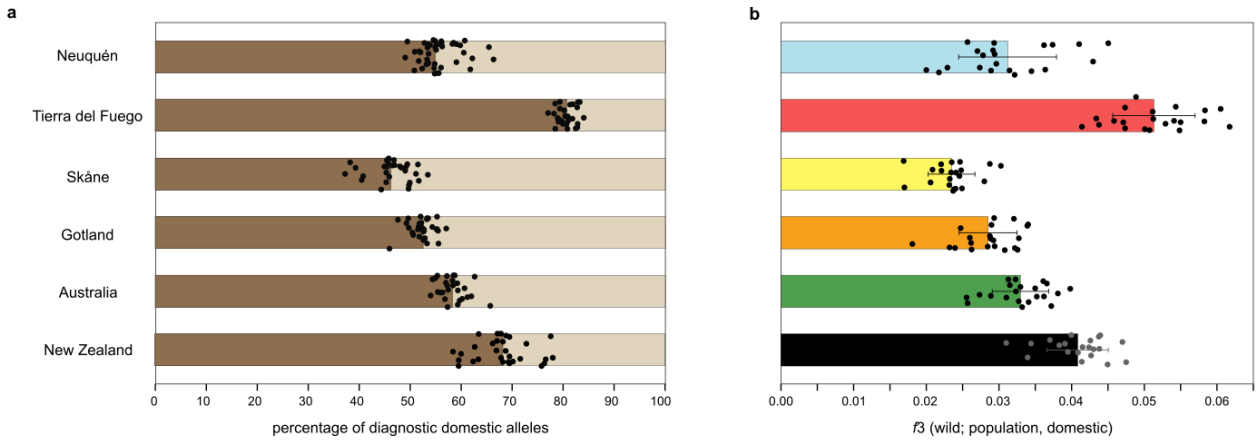


630 **Fig. 2 | Introduced rabbit populations have a large proportion of domestic ancestry. (A)**
631 Ancestry index representing the percentage of diagnostic domestic alleles per population (dark
632 brown) compared to wild alleles (light brown). Each dot corresponds to the percentage of domestic
633 alleles in each sampled individual; **(B)** Outgroup f_3 statistics calculated for all introduced
634 populations to measure shared drift between each introduced population and domestic rabbits to the
635 wild outgroup. Bar plot values represent the average value of *f*3 calculated for each chromosome
636 independently, and error bars indicate the standard deviation. Each dot corresponds to the average
637 *f*3 value for each chromosome.
638

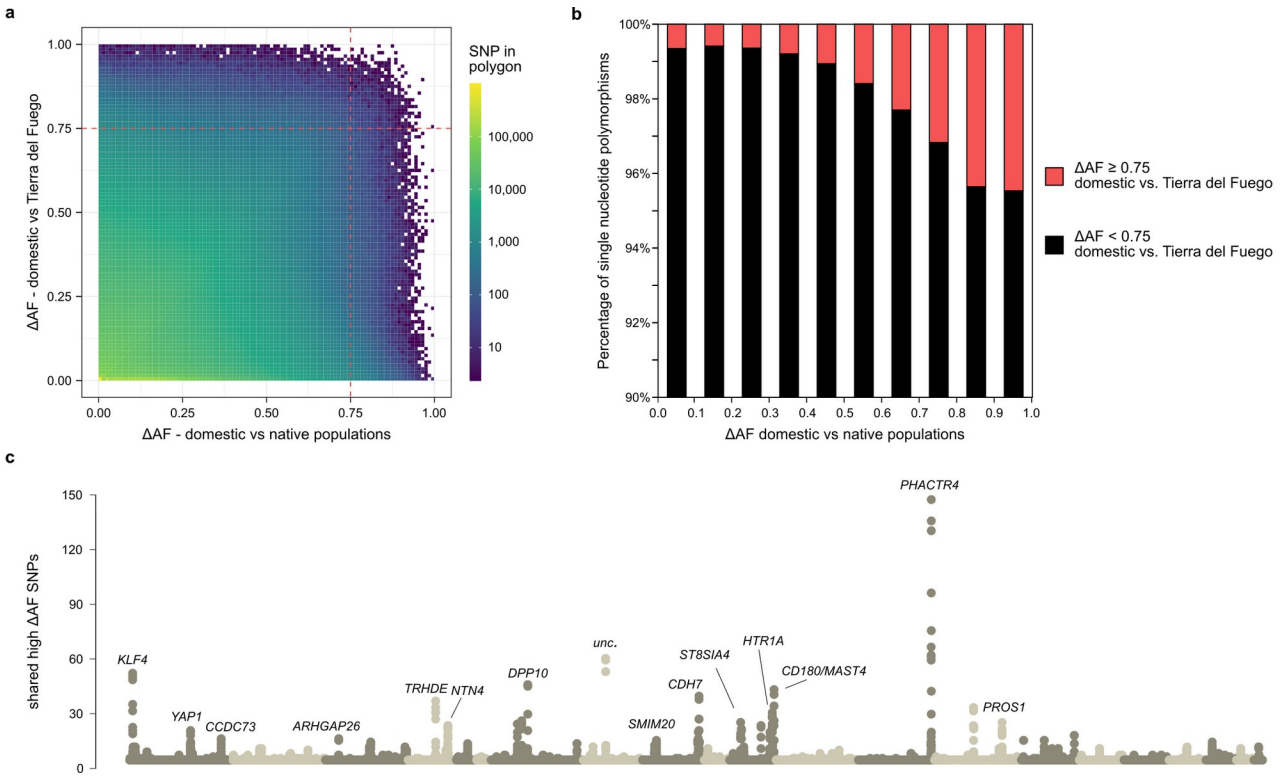
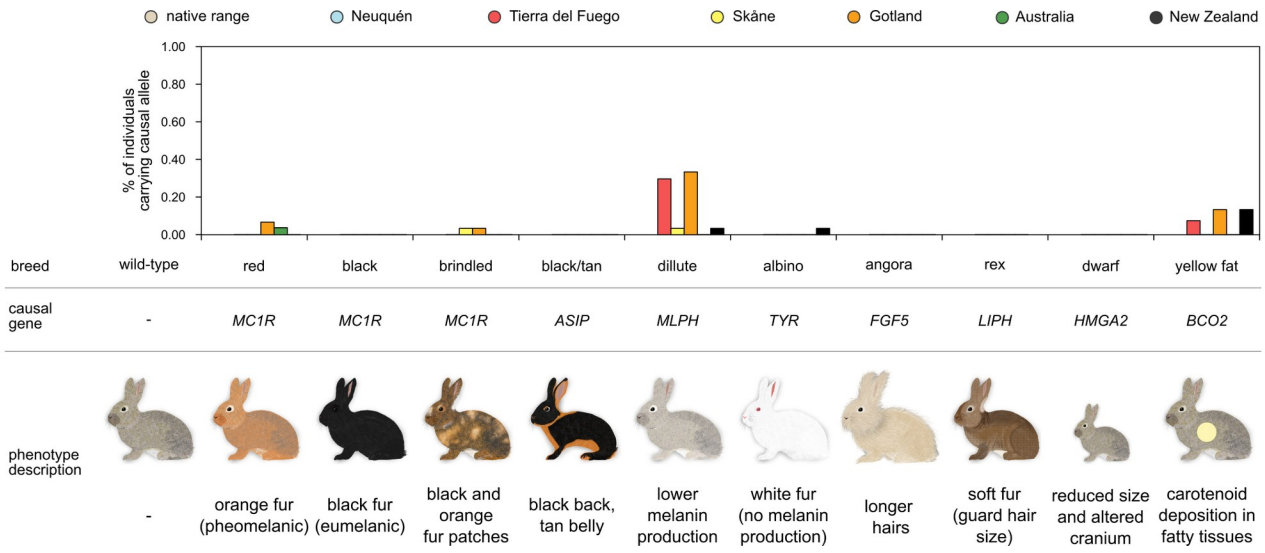
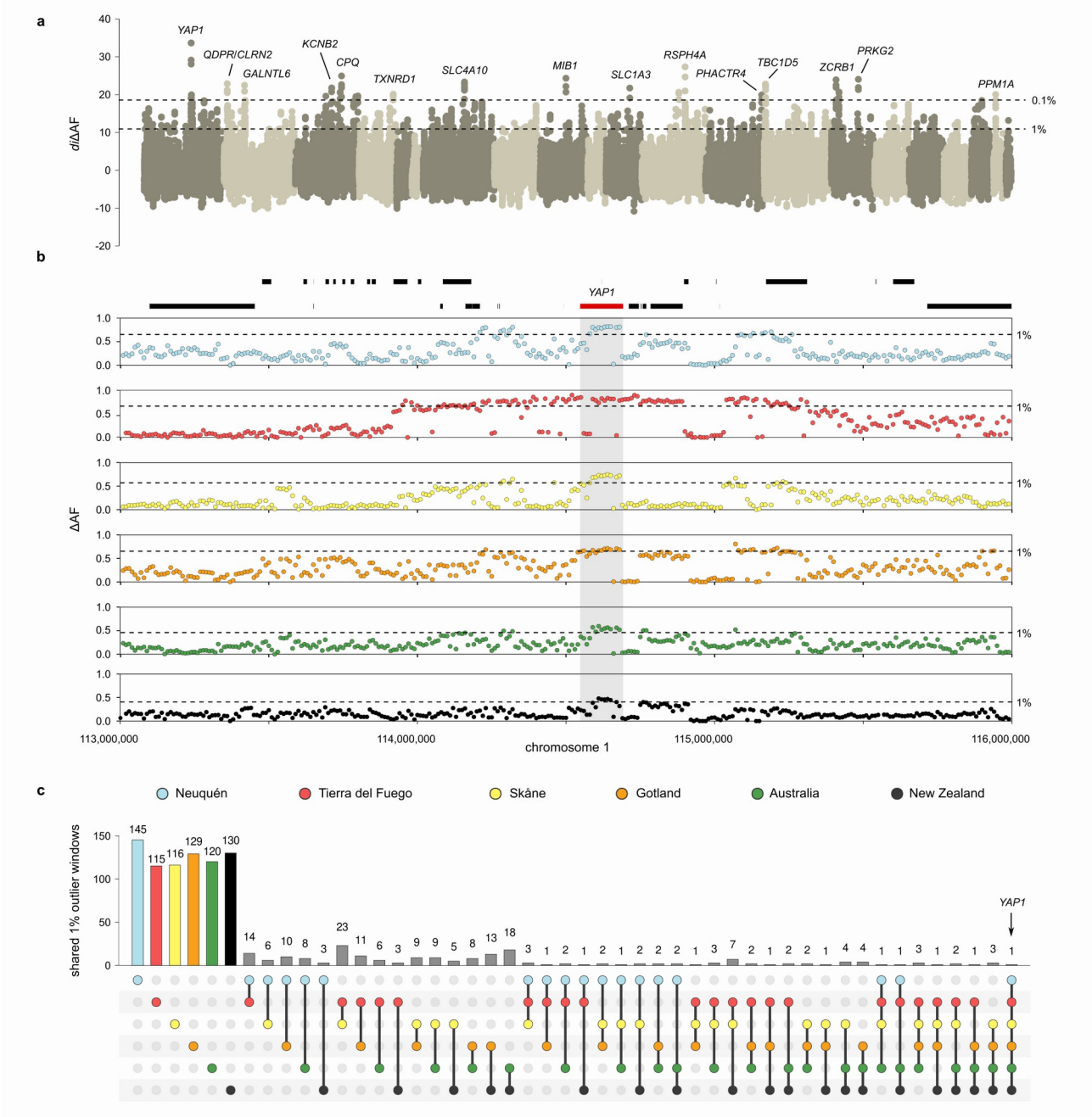


Fig. 3 | Adaptation in an introduced population with a predominant domestic ancestry (Tierra del Fuego). (A) Comparison between allele frequency differences (ΔAF) of domestic rabbits and native wild rabbits, to the domestic rabbits vs. Tierra del Fuego pair. The area of the plot is divided into 100x100 squares, with each square colored according to the density of single nucleotide polymorphisms (SNP) present at its coordinate. **(B)** Percentage of SNPs that have high (ΔAF ≥ 0.75, red) or low (ΔAF < 0.75, black) allele frequency differences between domestic rabbits and the Tierra del Fuego population, compared to their ΔAF in the domestic versus native comparison. This contrast is informative on whether SNPs that are associated with feralization in this population were also more likely to have been associated with domestication, or if feralization affects loci irrespective of their role in domestication. **(C)** Genome-wide distribution of SNP which have simultaneous high allele frequency differences (ΔAF ≥ 0.75) between domestic and native rabbits, and between domestic and rabbits from Tierra del Fuego. The y-axis shows counts of these variants for overlapping 100 kb windows (25 kb overlap). Genes with putative functional significance and overlapping the top signals are highlighted (unc. - uncharacterized protein-coding gene). Alternating colors correspond to different chromosomes.

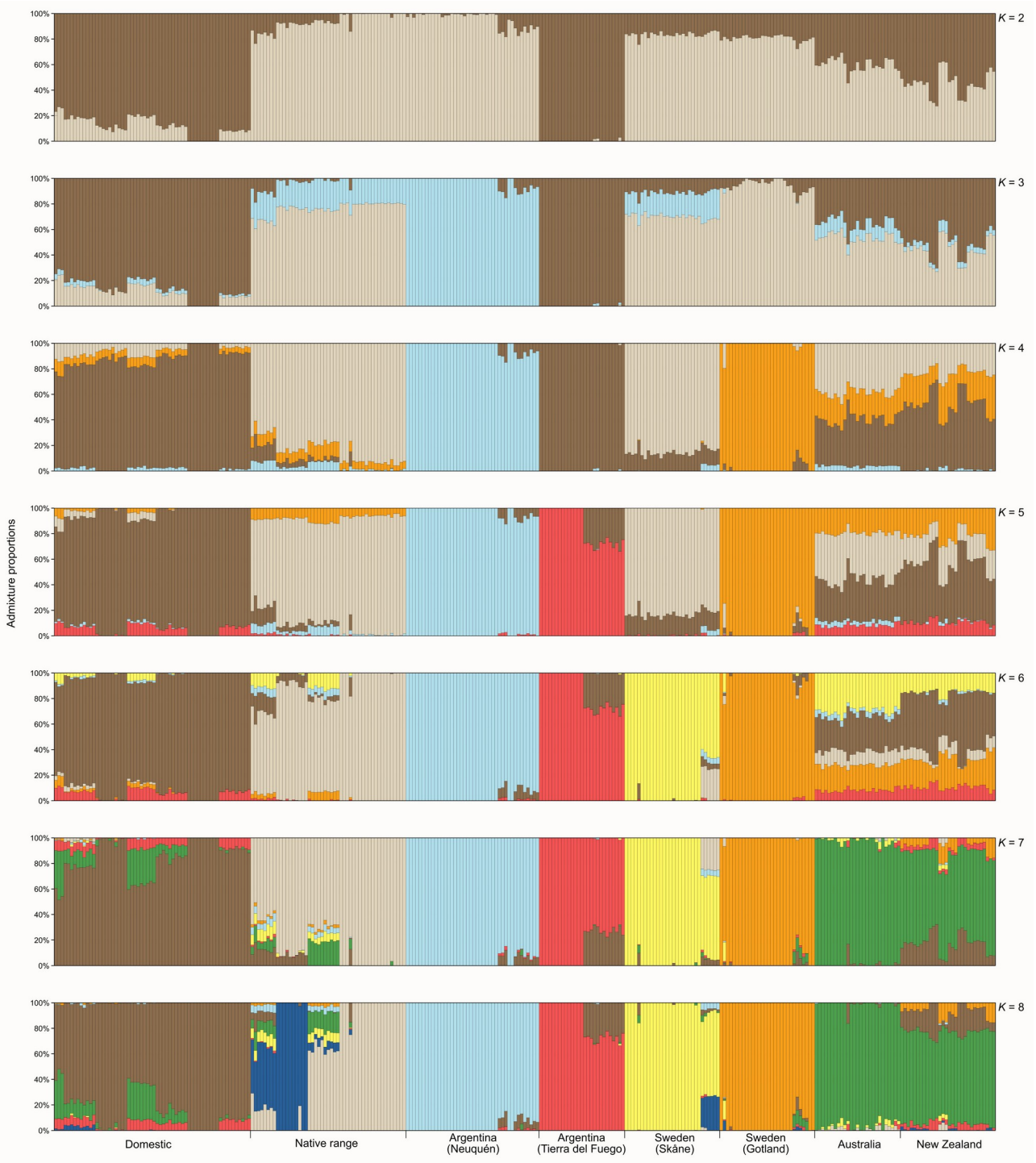


659 **Fig. 4 | Presence of mutations associated with multiple traits in domestic rabbits in the six**
660 **introduced populations**. The plot indicates the proportion of individuals carrying at least one
661 mutant allele. The information below the bars indicates the name of the breed, the implicated causal
662 gene, and a description of the phenotype associated with each mutation. Illustrations by Nuno
663 Guerra Serén.
664

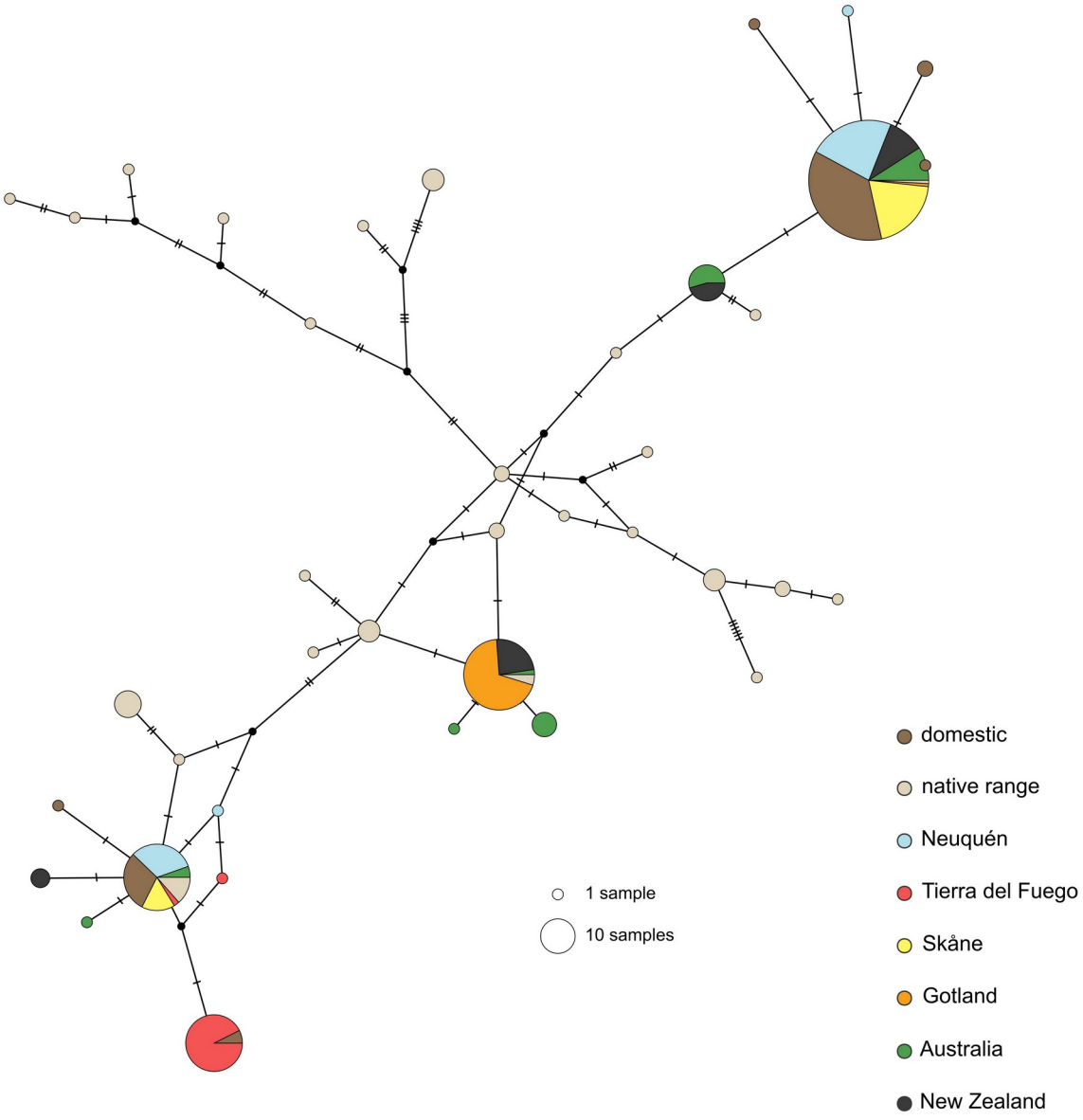


666 **Fig. 5 | Signatures of selection against domestic ancestry in introduced rabbit populations. (A)**
667 Scan for signatures of repeated genetic differentiation between domestic and introduced rabbits
668 across colonization events as measured by d_i (31). d_i was calculated from allele frequency
669 differences (d_iΔAF) between domestic rabbits and each population. Each dot represents 100 kb
670 windows with 25 kb steps iterated across the genome, and the dashed lines represent thresholds for
671 the top 1% and 0.1% outlier windows (from an empirical distribution considering only autosomal
672 regions). Genes of potential functional significance to adaptation to the wild, and overlapping the
673 top signals, are highlighted. **(B)** Allele frequency differences (ΔAF) between domestic and multiple
674 introduced populations overlapping *YAP1* (a candidate for parallel adaptation across populations).
675 The open reading frame of *YAP1* is highlighted by a red box, while that of the other protein-coding

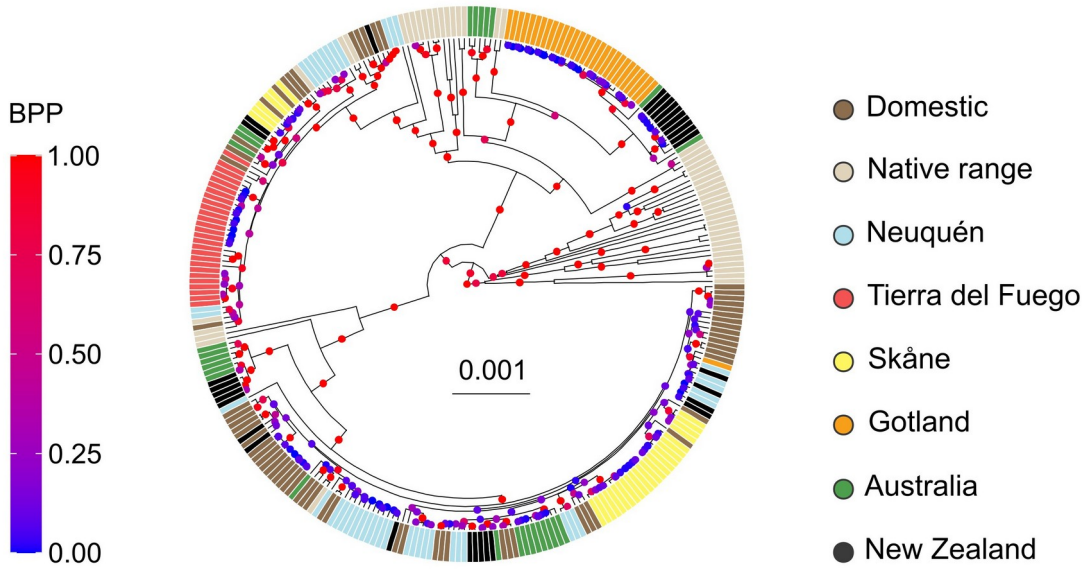
genes in the region are highlighted in black (genes on top are in the forward strand, on the bottom in the reverse strand). Contrasts with each population are labeled with a different color; each dot represents the median ΔAF from a non-overlapping 10 kb window. The dashed line represents the top 1% threshold of the empirical distribution in each contrast. **(C)** Population-specific and shared outlier windows from domestic vs. introduced ΔAF scans (100 kb non-overlapping windows). Colored dots indicate the existence of shared top 1% ΔAF outliers between different domestic-population contrasts, with the number of shared windows indicated above.



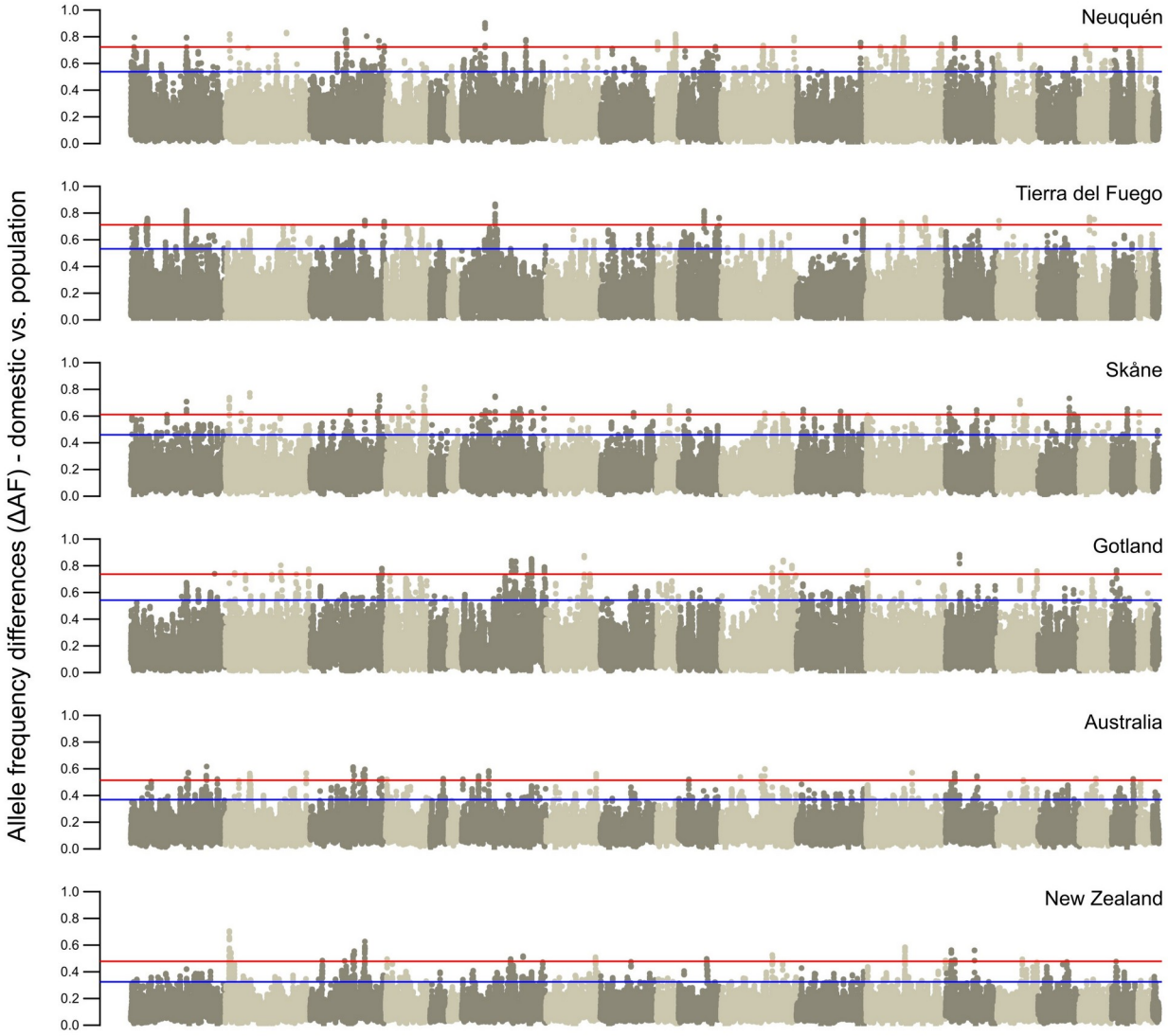
686 **Extended Data Fig. 1 | Admixture in introduced rabbit populations**. Admixture proportions
687 calculated for a sample of domestic rabbits, wild rabbits from the native range and six introduced
688 populations, based on genotype likelihoods. Results for several values of *K* are shown and the
689 population names are given at the bottom of the figure.
690



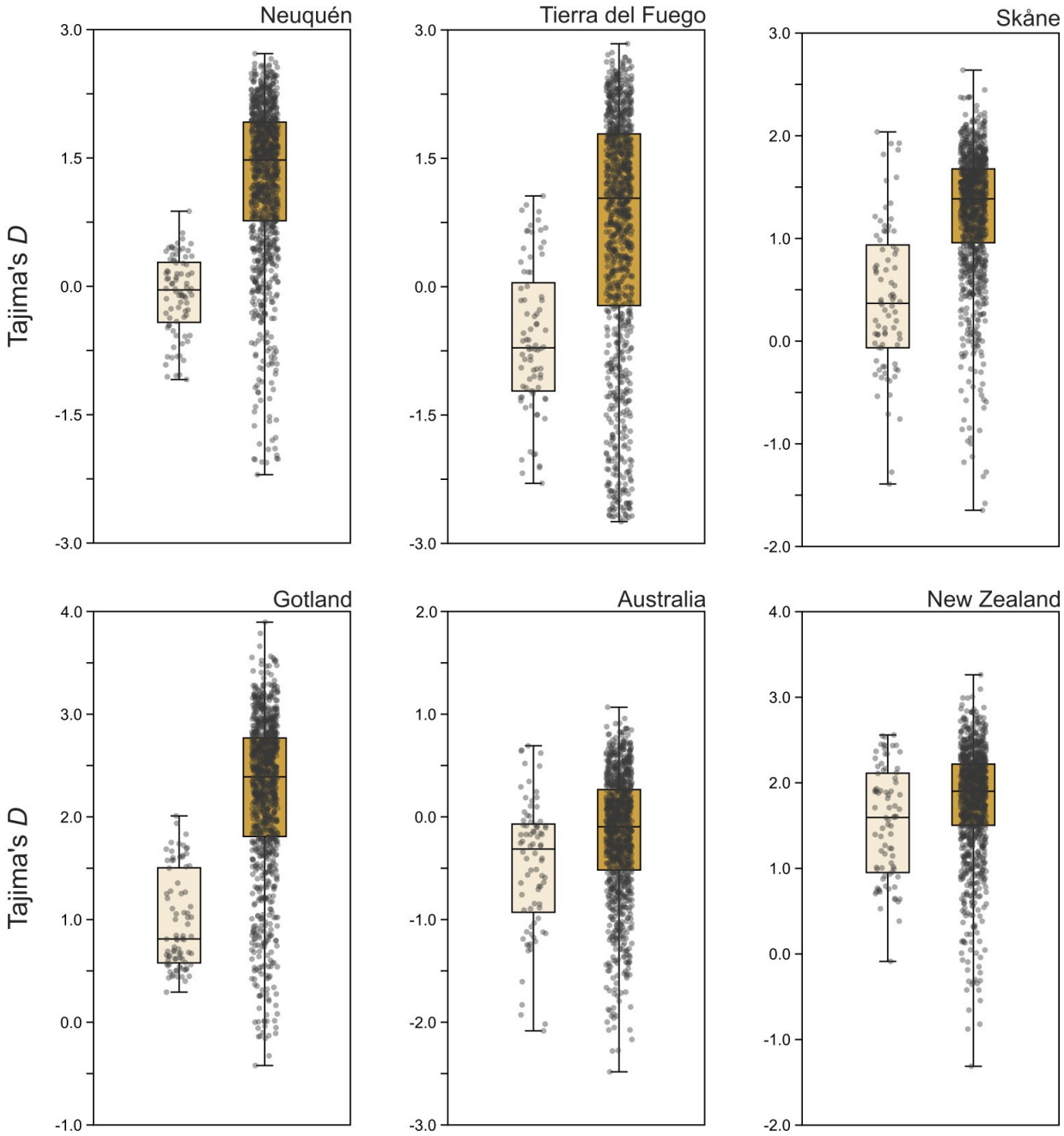
692 **Extended Data Fig. 2 | Median-joining haplotype network of the mtDNA cytochrome b locus.**
693 The size of the circle is proportional to the number of individuals that share the same haplotype.
694 The number of mutations for each branch is given by the number of smaller cross-dashes on the
695 branch.



Extended Data Fig. 3 | Bayesian tree of mtDNA sequences. Each individual is coloured according to the population of origin. Support values (Bayesian posterior probabilities, BPP) for each node are coloured according to the scale.



Extended Data Fig. 4 | Genome-wide differences in allele frequency (ΔAF) between domestic rabbits and each introduced population. Dots correspond to 100 kb windows, with a step of 25 kb. The red line corresponds to the top 0.1% of the empirical distribution for each contrast, while the blue line corresponds to the 1%. Only autosomes were considered due to the lower effective population size of the X chromosome, which results in higher-than-average differentiation for variants within that chromosome.



Extended Data Fig. 5 | Signatures of selection on genomic regions of high differentiation (differences in allele frequency, ΔAF) between domestic rabbits and each introduced population. For each introduced population we calculated Tajima's *D* in 100 kb windows, with a step of 25 kb. We then inspected *D* values for the top 0.1% ΔAF windows in each domestic-population contrast (light brown, left box in each plot, n = 82) and compared them to genome-wide *D* values (dark brown, right box in each plot, n = 1,000 randomly selected windows). For each plot, whisker ends represent minimum and maximum of the distribution; box edges represent first quartile and third quartile of the distribution; centre line represents the median. See Supplementary Table 3 for statistical testing on the full genome-wide dataset.

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TABLE OF CONTENTS

SUPPLEMENTARY TEXT

Records on the introduction of rabbit populations in the six populations from this study

South America

Populations of European rabbits were established in five regions of continental Argentina: south of San Juan, north of Mendoza, south of Mendoza and north of Neuquén, east of Chubut, and southwest of Santa Cruz province

Argentina - Neuquén

Within the general area where the provincial borders of Neuquén and Mendoza meet, the first established rabbit population was seen between 1945 and 1950 in the headwaters of the Neuquén River, near Andacollo locality in Neuquén province (36° 80′ W; Howard and Amaya 1975). These authors suggest that there is circumstantial evidence that rabbit populations in central Chile (brought from Spain) spread to Argentina crossing the Andes Cordillera through passes lower than 1800 m elevation. This dispersal probably occurred during summer, when environmental and habitat conditions were more suitable due to the presence of grass for food and shrubs for shelter (Jaksic et al. 2002). In 1969, Howard and Amaya (1975) recorded that rabbits crossed the Colorado River to the north (arriving in Mendoza province) and the Neuquén and Agrio rivers to the south.

Argentina - Tierra del Fuego

Delibes and Delibes-Mateos (2015) documented from a sailor's diary that in 1765 a ship named Purísima Concepción shipwrecked near the coast of Tierra del Fuego and the crew introduced rabbits in the island with the intention of being supplied with food. However, nothing is known about the success of this early introduction. In 1880, Thomas Bridges and his sons introduced rabbits in several islands in the Beagle Channel (Bridges 1949, in Jaksic and Yáñez 1983) to provide food to castaways and Yahgan (natives to the island) (Navas 1987). These individuals came from the Falkland (or Malvinas) islands, where they were introduced by French colonists around 1765 (Fig. 9.1).

Europe

Sweden - Skåne

Although there is anecdotal information about rabbits in Sweden tracing back to medieval times, likely domestic rabbits, the first documented introduction occurred in 1863 near Göteborg at the Swedish west coast. In the following years, during the 1870s and 1880s, there were reports about feral/wild rabbits from several places in southern Sweden, including Skåne and Gotland. The generally accepted first successful introductions of rabbits to Skåne occurred, however, in 1903, with some variation on the exact year (cf. Curry-Lindahl, 1970; Andersson et al., 1981; Danell, 2023).

Swedish wild rabbits are commonly believed to have originated from feral domestic rabbits, wild rabbits from central Europe and imports from European game farms. The primary rationale for rabbit introductions was to provide hunters with a novel game species. After a few decades however, the success of the rabbits raised a concern named "kaninfaran" in Swedish (Eng. "Rabbit Danger"), referring to the impact rabbits had on farming, forestry and gardening. The "Rabbit Danger" was likely exaggerated, and more recent studies indicate that the later impoverishment of the Swedish rabbit populations led to biodiversity losses (Eliasson, 1996; Larsson, 2006).

The current distribution includes most of south-central Sweden, including the Baltic Sea, and the islands Öland and Gotland (https://artfakta.se/artbestamning/taxon/oryctolagus-cuniculus-206005). North thereof it is possible to find isolated populations of recently established, and typically short-lived, feral rabbits. In recent years for example, the city of Gävle, located north of *limes norrlandicus*, (Rutger Sernander, sensu Fries, 1948), has experienced a rabbit population boost and subsequently decline because of rabbit hemorrhagic disease. Wild rabbits in Sweden also suffer from myxomatosis outbreaks, that has resulted in pauperized and fragmented populations with fluctuating densities.

Sweden - Gotland

According to Thamdrup (1965), rabbits were first introduced to Gotland in 1907 (thus, a few years after the south Swedish mainland), and in a few decades increased in numbers to cause problems for forestry and agriculture. There are, however, records of earlier introductions (see above), andrepeated introductions have likely occurred both before and after 1907.

After the spread of myxomatosis in 1962-63 (Curry-Lindahl, 1970) the population density of rabbits dropped dramatically. This had negative consequences for the royal eagle population on Gotland, for which rabbits are the most important prey species (Tjernberg 1981). In addition to

eagles, foxes also benefit from rabbit presence (Flux & Fullagar, 1992). There is also a local, domestic breed of rabbits called “Gotlandskanin” that might even predate wild rabbit occurrence.

Domestic rabbits have primarily been raised at Swedish farms since the nineteenth century, where they have been used for meat and fur production on a small scale. During the First and Second World Wars, rabbit production was an important food resource, and rabbit meat was also exported (*e.g.*, England). In general, however, domestic rabbits in Sweden are mostly raised as pet animals and are not relevant in the overall meat production.

Oceania

Australia

Major introduction from England of a mix of wild and domestic rabbits. Rabbits were released originally in Victoria followed by a fast spread (Alves et al. 2022).

New Zealand

Multiple introductions of domestic rabbits from 1777 onward and releases of wild type rabbits sourced from England and Australia from the late 1850s. Substantial contribution of domestic rabbits (Alves et al. 2022)

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SUPPLEMENTARY TABLES

Supplementary Table 1. Summary statistics of the whole-genome sequencing data.

Sample	Population	Breed/location	Number of reads	% of reads mapping	Depth of coverage
AA01	domestic	English silver	24,896,255	98.85	1.23
AA02	domestic	English silver	58,769,065	98.85	2.75
AA04	domestic	English silver	16,374,904	99.02	0.80
AC01	domestic	Champagne d'argent	45,861,067	98.72	2.17
AC02	domestic	Champagne d'argent	27,338,523	98.65	1.34
AC03	domestic	Champagne d'argent	33,382,686	98.78	1.65
AC04	domestic	Champagne d'argent	32,013,957	98.67	1.58
AC05	domestic	Champagne d'argent	24,345,063	98.58	1.20
AC06	domestic	Champagne d'argent	33,899,531	98.80	1.67
AC07	domestic	Champagne d'argent	22,429,864	98.81	1.11
AC08	domestic	Champagne d'argent	16,353,769	98.57	0.81
AC09	domestic	Champagne d'argent	32,709,384	98.75	1.62
AC10	domestic	Champagne d'argent	29,188,540	98.75	1.45
BH01	domestic	Belgian hare	17,080,737	98.80	0.85
BH02	domestic	Belgian hare	23,865,206	98.76	1.17
BH03	domestic	Belgian hare	26,889,182	98.77	1.32
BH04	domestic	Belgian hare	25,658,695	98.65	1.27
BH05	domestic	Belgian hare	22,595,656	98.71	1.11
BH06	domestic	Belgian hare	37,477,423	98.70	1.83
BH07	domestic	Belgian hare	27,051,125	98.74	1.33
BH08	domestic	Belgian hare	22,668,060	98.70	1.12
BH09	domestic	Belgian hare	17,006,563	98.65	0.84
BH10	domestic	Belgian hare	22,006,303	98.67	1.09
DUTCH01	domestic	Dutch	25,550,345	98.83	1.20
DUTCH03	domestic	Dutch	33,303,523	98.68	1.64
DUTCH04	domestic	Dutch	16,019,210	98.53	0.79
DUTCH05	domestic	Dutch	17,167,621	98.73	0.84
DUTCH06	domestic	Dutch	22,174,240	98.69	1.09
DUTCH07	domestic	Dutch	48,716,556	98.70	2.29
DUTCH08	domestic	Dutch	35,936,687	98.63	1.76
DUTCH11	domestic	Dutch	22,970,522	98.81	1.13
DUTCH12	domestic	Dutch	18,505,173	98.82	0.91

FGes01	domestic	Flemish giant	67,385,451	99.06	3.16
FGes02	domestic	Flemish giant	23,403,587	98.81	1.16
FGes05	domestic	Flemish giant	47,012,730	98.81	2.23
FGes10	domestic	Flemish giant	33,329,652	98.80	1.64
FGes11	domestic	Flemish giant	25,965,359	98.98	1.29
FGsap01	domestic	Flemish giant	16,120,576	98.78	0.79
FGsap09	domestic	Flemish giant	15,829,996	98.80	0.77
FGsap14	domestic	Flemish giant	30,827,606	98.80	1.47
FGsap15	domestic	Flemish giant	26,063,456	98.96	1.29
FGsap18	domestic	Flemish giant	25,313,575	98.90	1.26
FL01	domestic	French lop	36,335,390	98.80	1.79
FL02	domestic	French lop	28,545,708	98.79	1.41
FL03	domestic	French lop	31,090,619	98.70	1.54
FL04	domestic	French lop	28,539,745	98.71	1.41
FL05	domestic	French lop	36,495,738	98.73	1.80
FL06	domestic	French lop	21,328,448	98.81	1.06
FL07	domestic	French lop	21,488,774	98.78	1.07
FL08	domestic	French lop	24,570,456	98.75	1.22
FL09	domestic	French lop	40,411,132	98.86	1.99
FL10	domestic	French lop	24,478,018	98.50	1.20
NZ26	domestic	New Zealand white	30,832,378	98.98	1.53
NZ27	domestic	New Zealand white	32,492,646	98.72	1.60
NZ28	domestic	New Zealand white	41,006,669	98.79	2.01
NZ30	domestic	New Zealand white	31,714,189	98.95	1.57
NZ31	domestic	New Zealand white	31,651,105	98.84	1.56
NZ32	domestic	New Zealand white	33,615,306	98.92	1.66
NZ33	domestic	New Zealand white	43,178,929	98.80	2.10
NZ36	domestic	New Zealand white	42,145,221	98.89	2.05
NZ41	domestic	New Zealand white	30,947,042	98.93	1.53
NZ44	domestic	New Zealand white	28,655,626	98.65	1.39
Caum01	wild native range	Caumont, France	89,217,562	98.78	4.21
Caum02	wild native range	Caumont, France	25,866,273	98.94	1.26
Caum03	wild native range	Caumont, France	19,474,830	98.81	0.95
Caum04	wild native range	Caumont, France	40,973,352	98.97	1.99
Caum05	wild native range	Caumont, France	17,889,434	98.74	0.87

Caum06	wild native range	Caumont, France	54,741,642	99.17	2.53
Caum07	wild native range	Caumont, France	62,534,358	98.87	2.89
Caum10	wild native range	Caumont, France	23,005,786	98.81	1.10
LaRo01	wild native range	LaRoque, France	44,596,626	98.95	2.15
LaRo02	wild native range	LaRoque, France	57,732,587	98.92	2.77
LaRo03	wild native range	LaRoque, France	50,936,390	99.07	2.46
LaRo04	wild native range	LaRoque, France	37,205,892	98.95	1.79
LaRo05	wild native range	LaRoque, France	33,037,732	99.10	1.59
LaRo06	wild native range	LaRoque, France	48,214,072	99.04	2.34
LaRo07	wild native range	LaRoque, France	24,646,622	98.92	1.20
LaRo08	wild native range	LaRoque, France	41,006,038	98.94	1.98
LaRo09	wild native range	LaRoque, France	44,057,495	98.80	2.13
LaRo10	wild native range	LaRoque, France	49,837,202	98.81	2.39
TAR102	wild native range	Tarragona, Spain	12,513,082	99.09	0.55
TAR103	wild native range	Tarragona, Spain	24,460,826	98.90	1.08
TAR104	wild native range	Tarragona, Spain	18,531,082	99.02	0.82
TAR107	wild native range	Tarragona, Spain	21,020,848	99.06	0.92
TAR108	wild native range	Tarragona, Spain	44,315,228	99.06	1.94
TAR109	wild native range	Tarragona, Spain	14,233,146	98.75	0.64
TAR110	wild native range	Tarragona, Spain	15,304,440	99.09	0.67
TAR111	wild native range	Tarragona, Spain	26,086,380	98.68	1.14
TAR13	wild native range	Tarragona, Spain	28,408,490	99.49	0.88
TAR5	wild native range	Tarragona, Spain	13,792,534	98.89	0.60
TAR6	wild native range	Tarragona, Spain	14,436,527	99.02	0.63
Vill01	wild native range	Villemolaque, France	32,257,244	98.83	1.57
Vill02	wild native range	Villemolaque, France	34,508,971	98.90	1.67
Vill03	wild native range	Villemolaque, France	35,495,658	99.10	1.71
Vill04	wild native range	Villemolaque, France	39,560,871	98.75	1.92
Vill05	wild native range	Villemolaque, France	47,719,713	98.94	2.25
Vill06	wild native range	Villemolaque, France	33,918,572	98.92	1.65
Vill07	wild native range	Villemolaque, France	41,015,933	98.87	1.98
Vill08	wild native range	Villemolaque, France	22,379,477	98.89	1.09
Vill09	wild native range	Villemolaque, France	19,094,020	98.75	0.94
Vill10	wild native range	Villemolaque, France	17,692,142	98.85	0.87
ZRG1.2	wild native range	Zaragoza, Spain	15,518,465	99.42	0.66
ZRG11	wild native range	Zaragoza, Spain	9,439,899	99.07	0.41
ZRG12	wild native range	Zaragoza, Spain	39,906,085	99.28	1.50

ZRG14	wild native range	Zaragoza, Spain	16,501,975	99.17	0.71
ZRG15	wild native range	Zaragoza, Spain	9,606,534	99.28	0.41
ZRG17	wild native range	Zaragoza, Spain	8,803,508	99.26	0.36
ZRG18	wild native range	Zaragoza, Spain	17,093,656	99.44	0.72
ZRG21	wild native range	Zaragoza, Spain	8,347,950	99.45	0.35
ZRG4	wild native range	Zaragoza, Spain	17,831,937	98.81	0.78
ZRG5.2	wild native range	Zaragoza, Spain	22,084,918	99.07	0.96
OcAL02	Argentina (Neuquén)	Aluminé, Neuquén, Argentina	44,827,209	99.14	1.78
OcAL03	Argentina (Neuquén)	Aluminé, Neuquén, Argentina	17,895,130	96.81	0.76
OcAL04	Argentina (Neuquén)	Aluminé, Neuquén, Argentina	18,149,140	99.16	0.81
OcAL05	Argentina (Neuquén)	Aluminé, Neuquén, Argentina	20,768,798	99.47	0.95
OcAL06	Argentina (Neuquén)	Aluminé, Neuquén, Argentina	22,102,935	99.49	1.00
OcAL07	Argentina (Neuquén)	Aluminé, Neuquén, Argentina	19,872,865	99.47	0.86
OcAL08	Argentina (Neuquén)	Aluminé, Neuquén, Argentina	49,197,402	98.61	1.91
OcAL09	Argentina (Neuquén)	Aluminé, Neuquén, Argentina	10,809,625	98.82	0.41
OcAL10	Argentina (Neuquén)	Aluminé, Neuquén, Argentina	20,024,420	97.89	0.87
OcAL11	Argentina (Neuquén)	Aluminé, Neuquén, Argentina	16,624,578	99.35	0.75
OcAL12	Argentina (Neuquén)	Aluminé, Neuquén, Argentina	12,586,504	97.67	0.53
OcAL13	Argentina (Neuquén)	Aluminé, Neuquén, Argentina	49,237,679	99.17	2.06
OcAL15	Argentina (Neuquén)	Aluminé, Neuquén, Argentina	54,394,524	99.11	2.28
OCNEU10	Argentina (Neuquén)	Manzano Amargo, Neuquén, Argentina	35,596,773	99.01	1.67
OCNEU11	Argentina (Neuquén)	Manzano Amargo, Neuquén, Argentina	34,104,406	98.63	1.58
OCNEU12	Argentina (Neuquén)	Manzano Amargo, Neuquén, Argentina	46,449,831	99.16	2.18
OCNEU13	Argentina (Neuquén)	Manzano Amargo, Neuquén, Argentina	24,615,459	98.65	1.16
OCNEU14	Argentina (Neuquén)	Manzano Amargo, Neuquén, Argentina	19,440,520	99.08	0.91
OCNEU15	Argentina (Neuquén)	Manzano Amargo, Neuquén, Argentina	23,400,855	99.15	1.10
OCNEU16	Argentina (Neuquén)	Manzano Amargo, Neuquén, Argentina	25,251,990	95.58	1.04
OCNEU17	Argentina (Neuquén)	Manzano Amargo, Neuquén, Argentina	39,557,630	98.89	1.88
OCNEU18	Argentina (Neuquén)	Manzano Amargo, Neuquén, Argentina	36,599,905	98.41	1.66
OCNEU19	Argentina (Neuquén)	Manzano Amargo, Neuquén, Argentina	37,279,608	99.17	1.74
OCNEU20	Argentina (Neuquén)	Manzano Amargo, Neuquén, Argentina	27,142,114	99.22	1.24
OCNEU21	Argentina (Neuquén)	Manzano Amargo, Neuquén, Argentina	19,376,086	99.19	0.88
OCNEU36	Argentina (Neuquén)	Manzano Amargo, Neuquén, Argentina	37,318,394	98.78	1.74
OCNEU37	Argentina (Neuquén)	Manzano Amargo, Neuquén, Argentina	31,432,490	98.64	1.45
OCNEU38	Argentina (Neuquén)	Manzano Amargo, Neuquén, Argentina	34,070,250	99.08	1.58

OCNEU39	Argentina (Neuquén)	Manzano Amargo, Neuquén, Argentina	41,330,741	99.00	1.93
OCNEU40	Argentina (Neuquén)	Manzano Amargo, Neuquén, Argentina	34,878,314	98.97	1.64
OCNEU41	Argentina (Neuquén)	Manzano Amargo, Neuquén, Argentina	27,488,697	98.57	1.27
OCNEU42	Argentina (Neuquén)	Manzano Amargo, Neuquén, Argentina	62,391,137	98.96	2.88
OCNEU44	Argentina (Neuquén)	Manzano Amargo, Neuquén, Argentina	41,900,052	98.95	1.94
OCNEU45	Argentina (Neuquén)	Manzano Amargo, Neuquén, Argentina	40,604,655	98.57	1.86
OCNEU46	Argentina (Neuquén)	Manzano Amargo, Neuquén, Argentina	29,929,751	99.21	1.37
OCNEU47	Argentina (Neuquén)	Manzano Amargo, Neuquén, Argentina	26,896,244	99.22	1.21
OCNEU48	Argentina (Neuquén)	Manzano Amargo, Neuquén, Argentina	32,131,018	99.05	1.49
OCNEU49	Argentina (Neuquén)	Manzano Amargo, Neuquén, Argentina	35,668,852	99.24	1.63
OCNEU50	Argentina (Neuquén)	Manzano Amargo, Neuquén, Argentina	42,357,343	98.85	1.96
OCNEU7	Argentina (Neuquén)	Manzano Amargo, Neuquén, Argentina	24,769,255	98.95	1.17
OCNEU8	Argentina (Neuquén)	Manzano Amargo, Neuquén, Argentina	28,409,486	98.05	1.29
OCNEU9	Argentina (Neuquén)	Manzano Amargo, Neuquén, Argentina	22,411,105	99.09	1.05
OCTDF_17	Argentina (Tierra del Fuego)	Lapataia, Tierra del Fuego, Argentina	59,628,163	98.40	2.82
OCTDF_18	Argentina (Tierra del Fuego)	Lapataia, Tierra del Fuego, Argentina	46,808,442	99.23	2.22
OCTDF_19	Argentina (Tierra del Fuego)	Lapataia, Tierra del Fuego, Argentina	38,041,433	98.76	1.83
OCTDF_30	Argentina (Tierra del Fuego)	Lapataia, Tierra del Fuego, Argentina	37,412,364	98.92	1.80
OCTDF_31	Argentina (Tierra del Fuego)	Lapataia, Tierra del Fuego, Argentina	37,757,120	98.78	1.81
OCTDF0	Argentina (Tierra del Fuego)	Lapataia, Tierra del Fuego, Argentina	19,608,306	99.30	0.92
OCTDF2	Argentina (Tierra del Fuego)	Lapataia, Tierra del Fuego, Argentina	30,611,819	99.40	1.44
OCTDF3	Argentina (Tierra del Fuego)	Lapataia, Tierra del Fuego, Argentina	23,882,472	99.13	1.11
OCTDF4	Argentina (Tierra del Fuego)	Lapataia, Tierra del Fuego, Argentina	31,224,697	98.91	1.48
OCTDF5	Argentina (Tierra del Fuego)	Lapataia, Tierra del Fuego, Argentina	39,954,796	98.78	1.91
OCTDF6	Argentina (Tierra del Fuego)	Lapataia, Tierra del Fuego, Argentina	28,366,271	99.19	1.32
OCTDF7	Argentina (Tierra del Fuego)	Lapataia, Tierra del Fuego, Argentina	60,884,509	99.01	2.84
OCTDF8	Argentina (Tierra del Fuego)	Lapataia, Tierra del Fuego, Argentina	24,504,943	98.75	1.11
OCTDF9	Argentina (Tierra del Fuego)	Lapataia, Tierra del Fuego, Argentina	40,181,650	99.04	1.92
OcTF01	Argentina (Tierra del Fuego)	Estancia Túnel, Tierra del Fuego, Argentina	54,699,139	99.21	2.54
OcTF02	Argentina (Tierra del Fuego)	Estancia Túnel, Tierra del Fuego, Argentina	25,623,173	99.25	1.19
OcTF03	Argentina (Tierra del Fuego)	Estancia Túnel, Tierra del Fuego, Argentina	22,964,553	99.37	1.07
OcTF04	Argentina (Tierra del Fuego)	Estancia Túnel, Tierra del Fuego, Argentina	10,483,040	94.60	0.44
OcTF06	Argentina (Tierra del Fuego)	Estancia Túnel, Tierra del Fuego, Argentina	14,842,704	94.18	0.61
OcTF08	Argentina (Tierra del Fuego)	Estancia Túnel, Tierra del Fuego, Argentina	46,963,023	99.16	2.20
OcTF09	Argentina (Tierra del Fuego)	Estancia Túnel, Tierra del Fuego, Argentina	59,784,058	99.17	2.79
OcTF10	Argentina (Tierra del Fuego)	Estancia Túnel, Tierra del Fuego, Argentina	33,253,301	99.19	1.56
OcTF11	Argentina (Tierra del Fuego)	Estancia Túnel, Tierra del Fuego, Argentina	33,208,753	99.23	1.56

OcTF12	Argentina (Tierra del Fuego)	Estancia Túnel, Tierra del Fuego, Argentina	21,770,678	97.55	0.95
OcTF13	Argentina (Tierra del Fuego)	Estancia Túnel, Tierra del Fuego, Argentina	33,080,393	99.17	1.56
OcTF14	Argentina (Tierra del Fuego)	Estancia Túnel, Tierra del Fuego, Argentina	17,017,245	95.37	0.69
OcTF15	Argentina (Tierra del Fuego)	Estancia Túnel, Tierra del Fuego, Argentina	41,696,162	98.29	1.73
Occ-S-01	Sweden (Skåne)	Torekov (Burensvik), Skåne, Sweden	28,983,677	98.71	1.40
Occ-S-02	Sweden (Skåne)	Torekov (Burensvik), Skåne, Sweden	30,002,820	98.79	1.45
Occ-S-03	Sweden (Skåne)	Torekov (Burensvik), Skåne, Sweden	22,469,085	98.57	1.08
Occ-S-04	Sweden (Skåne)	Torekov (Burensvik), Skåne, Sweden	23,928,263	98.84	1.14
Occ-S-05	Sweden (Skåne)	Torekov (Burensvik), Skåne, Sweden	26,629,682	98.68	1.26
Occ-S-06	Sweden (Skåne)	Torekov (village), Skåne, Sweden	20,476,290	98.82	0.98
Occ-S-07	Sweden (Skåne)	Torekov (village), Skåne, Sweden	23,751,067	98.94	1.14
Occ-S-08	Sweden (Skåne)	Torekov (village), Skåne, Sweden	60,120,525	95.89	2.59
Occ-S-09	Sweden (Skåne)	Torekov (village), Skåne, Sweden	60,264,562	97.09	2.68
Occ-S-10	Sweden (Skåne)	Torekov (village), Skåne, Sweden	50,796,679	97.51	2.26
Occ-S-11	Sweden (Skåne)	Torekov (village), Skåne, Sweden	27,739,115	98.50	1.31
Occ-S-12	Sweden (Skåne)	Torekov (village), Skåne, Sweden	29,226,819	98.83	1.40
Occ-S-13	Sweden (Skåne)	Torekov (village), Skåne, Sweden	31,349,593	98.75	1.48
Occ-S-14	Sweden (Skåne)	Torekov (village), Skåne, Sweden	36,669,601	98.77	1.73
Occ-S-15	Sweden (Skåne)	Torekov (village), Skåne, Sweden	34,808,238	98.70	1.67
Occ-S-16	Sweden (Skåne)	Torekov (village), Skåne, Sweden	22,190,141	98.76	1.08
Occ-S-17	Sweden (Skåne)	Torekov (village), Skåne, Sweden	23,277,418	98.96	1.13
Occ-S-18	Sweden (Skåne)	Torekov (village), Skåne, Sweden	28,065,919	98.66	1.35
Occ-S-19	Sweden (Skåne)	Torekov (village), Skåne, Sweden	21,000,911	98.77	1.02
Occ-S-20	Sweden (Skåne)	Torekov (village), Skåne, Sweden	22,594,997	98.73	1.09
Occ-S-21	Sweden (Skåne)	Torekov (village), Skåne, Sweden	21,974,295	98.80	1.06
Occ-S-22	Sweden (Skåne)	Torekov (village), Skåne, Sweden	50,563,013	98.16	2.28
Occ-S-23	Sweden (Skåne)	Torekov (village), Skåne, Sweden	19,806,562	98.73	0.95
Occ-S-24	Sweden (Skåne)	Torekov (village), Skåne, Sweden	35,571,202	98.76	1.68
Occ-S-25	Sweden (Skåne)	Näsbyholm, Skåne, Sweden	37,246,900	98.86	1.78
Occ-S-26	Sweden (Skåne)	Näsbyholm, Skåne, Sweden	37,952,570	98.65	1.80
Occ-S-27	Sweden (Skåne)	Näsbyholm, Skåne, Sweden	39,586,941	98.58	1.87
Occ-S-28	Sweden (Skåne)	Näsbyholm, Skåne, Sweden	49,169,995	98.92	2.32
Occ-S-29	Sweden (Skåne)	Näsbyholm, Skåne, Sweden	43,212,292	99.13	2.06
Occ-S-30	Sweden (Skåne)	Näsbyholm, Skåne, Sweden	46,482,587	99.03	2.20
Occ-S-48	Sweden (Gotland)	Hellvi (Hide), Gotland, Sweden	18,411,295	98.50	0.90
Occ-S-49	Sweden (Gotland)	Hellvi (Hide), Gotland, Sweden	28,636,645	98.77	1.39
Occ-S-50	Sweden (Gotland)	Hellvi (Hide), Gotland, Sweden	19,024,037	98.60	0.92

Occ-S-51	Sweden (Gotland)	Hellvi (Hide), Gotland, Sweden	26,136,643	98.63	1.26
Occ-S-52	Sweden (Gotland)	Hellvi (Hide), Gotland, Sweden	25,484,002	98.66	1.23
Occ-S-53	Sweden (Gotland)	Hellvi (Hide), Gotland, Sweden	27,169,608	98.68	1.32
Occ-S-54	Sweden (Gotland)	Hellvi (Hide), Gotland, Sweden	29,667,274	98.69	1.42
Occ-S-55	Sweden (Gotland)	Hellvi (Hide), Gotland, Sweden	26,673,278	98.57	1.28
Occ-S-56	Sweden (Gotland)	Hellvi (St Olofsholm), Gotland, Sweden	27,598,868	98.62	1.33
Occ-S-57	Sweden (Gotland)	Hellvi (St Olofsholm), Gotland, Sweden	26,867,960	98.49	1.30
Occ-S-58	Sweden (Gotland)	Hellvi (St Olofsholm), Gotland, Sweden	29,539,196	98.59	1.42
Occ-S-59	Sweden (Gotland)	Hellvi (St Olofsholm), Gotland, Sweden	21,632,719	98.53	1.05
Occ-S-60	Sweden (Gotland)	Hellvi (St Olofsholm), Gotland, Sweden	33,820,359	98.56	1.62
Occ-S-61	Sweden (Gotland)	Hellvi (St Olofsholm), Gotland, Sweden	26,149,964	98.55	1.27
Occ-S-62	Sweden (Gotland)	Hellvi (St Olofsholm), Gotland, Sweden	27,467,452	98.60	1.33
Occ-S-63	Sweden (Gotland)	Hellvi (St Olofsholm), Gotland, Sweden	23,893,212	98.58	1.16
Occ-S-64	Sweden (Gotland)	Hellvi (St Olofsholm), Gotland, Sweden	22,305,337	98.62	1.09
Occ-S-65	Sweden (Gotland)	Hellvi (St Olofsholm), Gotland, Sweden	19,490,396	98.51	0.95
Occ-S-66	Sweden (Gotland)	Hellvi (St Olofsholm), Gotland, Sweden	37,203,838	98.55	1.79
Occ-S-67	Sweden (Gotland)	Hellvi (St Olofsholm), Gotland, Sweden	41,457,471	98.61	1.99
Occ-S-68	Sweden (Gotland)	Hellvi (St Olofsholm), Gotland, Sweden	33,235,525	98.59	1.60
Occ-S-69	Sweden (Gotland)	Fröjel (Mulde), Gotland, Sweden	21,715,154	98.70	1.06
Occ-S-70	Sweden (Gotland)	Fröjel (Mulde), Gotland, Sweden	26,997,473	98.64	1.30
Occ-S-71	Sweden (Gotland)	Fröjel (Mulde), Gotland, Sweden	29,703,472	98.60	1.43
Occ-S-72	Sweden (Gotland)	Fröjel (Mulde), Gotland, Sweden	43,602,406	98.55	2.09
Occ-S-73	Sweden (Gotland)	Fröjel (Mulde), Gotland, Sweden	35,469,570	98.51	1.69
Occ-S-74	Sweden (Gotland)	Fröjel (Mulde), Gotland, Sweden	24,230,993	98.68	1.16
Occ-S-75	Sweden (Gotland)	Fröjel (Mulde), Gotland, Sweden	39,497,654	98.61	1.89
Occ-S-76	Sweden (Gotland)	Fröjel (Mulde), Gotland, Sweden	28,306,944	98.55	1.36
Occ-S-77	Sweden (Gotland)	Fröjel (Mulde), Gotland, Sweden	37,952,906	98.53	1.82
VIC01	Australia	Wangaratta, Victoria, Australia	30,040,838	98.84	1.35
VIC02	Australia	Longwood, Victoria, Australia	54,217,624	98.81	2.42
VIC03	Australia	Wonwonda, Victoria, Australia	25,717,573	99.33	1.08
VIC05	Australia	Elmhurst, Victoria, Australia	45,026,681	98.58	2.03
VIC06	Australia	Bahgallah, Victoria, Australia	19,969,208	99.17	0.96
VIC07	Australia	Nelson, Victoria, Australia	33,900,523	99.49	1.53
VIC08	Australia	Cranbourne, Victoria, Australia	21,928,731	99.36	0.98
VIC09	Australia	Cranbourne South, Victoria, Australia	19,262,535	99.34	0.92
VIC10	Australia	Mt Moriac, Victoria, Australia	10,914,151	90.93	0.44

VIC11	Australia	Somers, Victoria, Australia	12,658,292	96.47	0.55
VIC12	Australia	Newhaven, Victoria, Australia	26,984,325	98.3	1.22
VIC13	Australia	Bendigo, Victoria, Australia	39,787,408	99.24	1.78
VIC14	Australia	Bendigo, Victoria, Australia	33,528,792	99.21	1.33
VIC16	Australia	Bacchus Marsh, Victoria, Australia	84,886,850	98.86	3.85
VIC17	Australia	Hattah, Victoria, Australia	37,662,682	99.16	1.81
VIC18	Australia	Hattah, Victoria, Australia	33,556,771	99.18	1.57
VIC19	Australia	Ararat, Victoria, Australia	37,923,897	98.94	1.82
VIC20	Australia	Ararat, Victoria, Australia	29,195,404	99.15	1.42
VIC21	Australia	Telopea Downs, Victoria, Australia	42,571,328	99.07	2.02
VIC22	Australia	Telopea Downs, Victoria, Australia	58,140,819	96.01	2.45
VIC23	Australia	Euroa, Victoria, Australia	58,255,830	96.03	2.52
VIC24	Australia	Euroa, Victoria, Australia	19,481,971	98.91	0.92
VIC25	Australia	Yambuk, Victoria, Australia	26,335,194	96.00	1.06
VIC27	Australia	Avalon, Victoria, Australia	17,008,836	97.91	0.71
VIC28	Australia	Avalon, Victoria, Australia	17,546,536	98.88	0.84
VIC29	Australia	Kerang, Victoria, Australia	52,878,593	97.41	2.37
VIC30	Australia	Pyramid Hill, Victoria, Australia	17,732,971	98.88	0.77
NZ_01	New Zealand	Bendigo new, Otago, New Zealand	34,737,992	99.17	1.66
NZ_02	New Zealand	Bendigo new, Otago, New Zealand	27,392,888	99.08	1.32
NZ_03	New Zealand	Bendigo new, Otago, New Zealand	34,497,936	99.37	1.65
NZ_04	New Zealand	Bendigo station, Otago, New Zealand	52,461,872	98.84	2.51
NZ_05	New Zealand	Bendigo station, Otago, New Zealand	28,135,278	98.86	1.36
NZ_06	New Zealand	Bendigo station, Otago, New Zealand	29,882,358	98.64	1.45
NZ_11	New Zealand	Cloudy peak station, Otago, New Zealand	17,943,224	98.91	0.86
NZ_12	New Zealand	Cloudy peak station, Otago, New Zealand	25,980,347	98.58	1.26
NZ_13	New Zealand	Cloudy peak station, Otago, New Zealand	48,475,423	98.90	2.32
NZ_14	New Zealand	Halswell H2, Canterbury, New Zealand	40,863,104	98.87	1.97
NZ_15	New Zealand	Halswell H3, Canterbury, New Zealand	22,703,835	98.98	1.10
NZ_16	New Zealand	Halswell H5, Canterbury, New Zealand	23,609,073	98.99	1.15
NZ_17	New Zealand	Lesley Hills, Canterbury, New Zealand	24,294,961	98.91	1.18
NZ_18	New Zealand	Lesley Hills, Canterbury, New Zealand	20,793,044	98.81	1.01
NZ_19	New Zealand	Lesley Hills, Canterbury, New Zealand	21,812,545	98.87	1.06
NZ_31	New Zealand	Queensberry hills, Otago, New Zealand	27,747,696	98.9	1.34
NZ_32	New Zealand	Queensberry hills, Otago, New Zealand	37,752,396	98.68	1.80
NZ_33	New Zealand	Queensberry hills, Otago, New Zealand	25,133,685	99.01	1.20
NZ_34	New Zealand	Selwyn Motukarara, Canterbury, New Zealand	25,450,611	98.78	1.22

NZ_35	New Zealand	Selwyn Motukarara, Canterbury, New Zealand	30,062,067	98.90	1.44
NZ_36	New Zealand	Selwyn Motukarara, Canterbury, New Zealand	33,355,750	98.93	1.59
NZ_37	New Zealand	Simons Hill, Canterbury, New Zealand	27,051,996	98.87	1.30
NZ_38	New Zealand	Simons Hill, Canterbury, New Zealand	22,990,402	98.79	1.11
NZ_39	New Zealand	Simons Hill, Canterbury, New Zealand	27,248,281	98.87	1.31
NZ_43	New Zealand	Tek River, Canterbury, New Zealand	25,363,074	98.61	1.23
NZ_44	New Zealand	Tek River, Canterbury, New Zealand	25,958,485	98.80	1.26
NZ_45	New Zealand	Tek River, Canterbury, New Zealand	23,174,109	98.81	1.13
NZ_46	New Zealand	Wantwood Station Gore, Southland, New Zealand	24,095,370	98.65	1.17
NZ_47	New Zealand	Wantwood Station Gore, Southland, New Zealand	28,529,999	98.54	1.39
NZ_48	New Zealand	Wantwood Station Gore, Southland, New Zealand	24,397,255	98.70	1.19

Supplementary Table 2. Average percentage of diagnostic domestic alleles in each of the six introduced populations in this study, based on a reference panel of 1,995 SNPs with allele frequency differences between domestic and wild samples above 0.9.

Population	Average percentage of diagnostic domestic alleles (%)	Standard deviation of the percentage of domestic alleles (%)
Argentina (Neuquén)	54.4	4.1
Argentina (Tierra del Fuego)	80.8	1.9
Sweden (Skåne)	47.5	4.2
Sweden (Gotland)	52.1	2.6
Australia	58.7	3.2
New Zealand	68.0	5.6

Supplementary Table 3. Welch's two-sided *t*-test results for the comparisons between genome-wide Tajima's *D* versus the top 0.1% windows in the allele frequency difference scan (ΔAF) between domestic rabbits and each introduced population. Both statistics were calculated in 100 kb windows, with a step of 25 kb. We then inspected *D* values for the top 0.1% ΔAF windows in each domestic-population contrast and compared them to genome-wide *D* values (n = 81,842 total windows). See Extended Data Fig.5 for more information.

Population	Welch's *t*	df	*P*	mean *D* (genome-wide)	mean *D* (top 0.1% ΔAF)	95% CI for mean difference	Hedge's *g*
Neuquén	25.77	81.67	$< 1.0 \times 10^{-15}$	1.212	-0.098	1.209 - 1.412	-1.407
Tierra del Fuego	13.89	81.48	$< 1.0 \times 10^{-15}$	0.703	-0.603	1.118 - 1.492	-0.896
Skåne	10.30	81.12	$< 1.0 \times 10^{-15}$	1.236	0.417	0.661 - 0.977	-1.318
Gotland	23.79	81.42	$< 1.0 \times 10^{-15}$	2.219	0.978	1.137 - 1.344	-1.638
Australia	3.99	81.15	1.423×10^{-4}	-0.189	-0.470	0.141 - 0.420	-0.465
New Zealand	3.65	81.15	4.657×10^{-4}	1.790	1.529	0.119 - 0.403	-0.416

Supplementary Table 4. Test for significant overlap between outliers in allele frequency differences (ΔAF) in contrasts of domestic vs. introduced populations. We calculated ΔAF in non-overlapping 100 kb windows and for each population retrieved the top 1% windows (205 in each population out of a total of 20,483 windows). Overlaps were tested with the *R* package *SuperExactTest*, which employs an algorithm for the calculation of the exact probability (one-sided) distributions of multi-set intersections. Bonferroni-corrected *P*-values are shown (significance at P < 0.05). Population abbreviations: NEU - Neuquén (Argentina); TDF - Tierra del Fuego (Argentina); SKA - Skåne (Sweden); GOT - Gotland (Sweden); AUS - Australia; NZE - New Zealand.

Populations	Degree of overlap	Observed overlap	Expected overlap	Fold-enrichment	P-value
NEU - NZE	2	10	2.052	4.874	0.002
NEU - GOT	2	16	2.052	7.798	1.558E-08
NEU - SKA	2	16	2.052	7.798	1.558E-08
NEU - AUS	2	18	2.052	8.773	1.570E-10
TDF - NZE	2	20	2.052	9.748	1.224E-12
TDF - GOT	2	22	2.052	10.723	7.532E-15
SKA - GOT	2	23	2.052	11.210	5.436E-16
TDF - AUS	2	24	2.052	11.698	3.719E-17
NEU - TDF	2	24	2.052	11.698	3.719E-17
GOT - NZE	2	25	2.052	12.185	2.417E-18
GOT - AUS	2	26	2.052	12.672	1.494E-19
SKA - NZE	2	26	2.052	12.672	1.494E-19
SKA - AUS	2	29	2.052	14.135	2.647E-23
AUS - NZE	2	38	2.052	18.521	1.419E-35
TDF - SKA	2	45	2.052	21.933	4.699E-46
NEU - GOT - NZE	3	1	0.021	48.700	1.000
NEU - TDF - GOT	3	2	0.021	97.399	0.012
NEU - GOT - AUS	3	3	0.021	146.099	7.758E-05
NEU - SKA - NZE	3	3	0.021	146.099	7.758E-05
NEU - SKA - AUS	3	3	0.021	146.099	7.758E-05
NEU - SKA - GOT	3	3	0.021	146.099	7.758E-05
NEU - TDF - NZE	3	3	0.021	146.099	7.758E-05
TDF - GOT - NZE	3	4	0.021	194.798	3.808E-07
NEU - AUS - NZE	3	4	0.021	194.798	3.808E-07
NEU - TDF - AUS	3	5	0.021	243.498	1.474E-09

NEU - TDF - SKA	3	5	0.021	243.498	1.474E-09
SKA - GOT - NZE	3	6	0.021	292.198	4.686E-12
TDF - SKA - GOT	3	6	0.021	292.198	4.686E-12
TDF - AUS - NZE	3	7	0.021	340.897	1.258E-14
TDF - GOT - AUS	3	7	0.021	340.897	1.258E-14
GOT - AUS - NZE	3	9	0.021	438.297	5.900E-20
SKA - GOT - AUS	3	9	0.021	438.297	5.900E-20
SKA - AUS - NZE	3	10	0.021	486.996	1.060E-22
TDF - SKA - AUS	3	10	0.021	486.996	1.060E-22
TDF - SKA - NZE	3	11	0.021	535.696	1.705E-25
NEU - GOT - AUS - NZE	4	1	0.000	4865.923	0.012
NEU - SKA - AUS - NZE	4	1	0.000	4865.923	0.012
NEU - SKA - GOT - NZE	4	1	0.000	4865.923	0.012
NEU - SKA - GOT - AUS	4	1	0.000	4865.923	0.012
NEU - TDF - GOT - NZE	4	1	0.000	4865.923	0.012
NEU - TDF - GOT - AUS	4	1	0.000	4865.923	0.012
NEU - TDF - SKA - NZE	4	1	0.000	4865.923	0.012
NEU - TDF - SKA - GOT	4	1	0.000	4865.923	0.012
TDF - GOT - AUS - NZE	4	2	0.000	9731.846	1.180E-06
TDF - SKA - GOT - NZE	4	2	0.000	9731.846	1.180E-06
NEU - TDF - AUS - NZE	4	2	0.000	9731.846	1.180E-06
NEU - TDF - SKA - AUS	4	2	0.000	9731.846	1.180E-06
TDF - SKA - AUS - NZE	4	3	0.000	14597.770	7.777E-11
SKA - GOT - AUS - NZE	4	4	0.000	19463.693	3.769E-15
TDF - SKA - GOT - AUS	4	4	0.000	19463.693	3.769E-15
TDF - SKA - GOT - AUS - NZE	5	1	0.000	486188.805	1.172E-04
NEU - SKA - GOT - AUS - NZE	5	1	0.000	486188.805	1.172E-04
NEU - TDF - GOT - AUS - NZE	5	1	0.000	486188.805	1.172E-04
NEU - TDF - SKA - AUS - NZE	5	1	0.000	486188.805	1.172E-04
NEU - TDF - SKA - GOT - NZE	5	1	0.000	486188.805	1.172E-04
NEU - TDF - SKA - GOT - AUS	5	1	0.000	486188.805	1.172E-04
NEU - TDF - SKA - GOT - AUS - NZE	6	1	0.000	48578562.424	1.173E-06