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The impacts of European arrival on Australian dingoes

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The European colonial expansion had dramatic consequences on both Indigenous Peoples and local fauna. In Australia, the degree to which the arrival of Europeans and their dogs impacted the ecology and ancestry of dingoes is contentious. To test for gene flow with European dogs, we sequenced genomes of 18 ancient Australian dingoes from the Nullarbor Plain, two early 20th-century New Guinean dingoes, a mid-19th-century kangaroo hound, and 33 contemporary dingoes from across Australia. To quantify dietary shifts after the arrival of the First Fleet (AD1788), we generated stable isotopic (δ^{13}C, δ^{15}N) data for 55 directly dated ancient Australian dingoes spanning the last ~2,300 y. We show that the diet of Nullarbor Plain dingoes shifted soon after European arrival, possibly due to shifts in prey abundance. Our genomic analyses demonstrated that pre-European dingoes were more inbred than most contemporary dog breeds, possibly as a result of population bottlenecks. We also showed that many dingoes, particularly those from Southeast Australia, experienced admixture with European dogs. Although we detected European ancestry dating to the early 18th-century, the majority of gene flow events coincided with the initiation of landscape-scale population control in the 1960s. Furthermore, some European dog alleles may have provided adaptive benefits to dingoes and alleviated inbreeding depression. Despite the existence of gene flow with European dogs, dingoes have maintained their distinctiveness. This suggests that management strategies should prioritize maintenance of substantial population sizes across Australia to both facilitate effective purifying and positive selection on introgressed alleles, and mitigate inbreeding.

paleogenomics | admixture | stable dietary isotopes | inbreeding | conservation

Significance

Though European colonization has dramatically altered the Australian landscape, the impact of these changes on populations such as dingoes remains contentious. By analyzing ancient DNA and stable isotopes from dingoes spanning the last 2,300 y, we showed dingoes shifted their diets after AD 1788, likely due to changes in prey abundance associated with introduced animals and landscape alteration. We also detected admixture between dingoes and introduced European dogs, largely during the 1960s. Our results suggest that this may have provided some benefit to dingoes by mediating the effects of inbreeding. This suggests that maintenance of sufficiently large wild populations of dingoes, in which natural selection can purge deleterious variation, while maintaining beneficial variation, is critical to ensure their long-term viability.

Dingoes are a free-living population descended from East Asian domestic dogs (1–4). Since their introduction to Australia and New Guinea (i.e., Sahul) over 3,000 y ago (5–8), they have established themselves in a wide range of environments including New Guinean high-altitude rainforests and arid Australian deserts. Although their impact on the ecosystem today is debated (9–11), the extended presence of dingoes in Sahul, and their role as the largest terrestrial predator, means they have acquired unique morphological and behavioral adaptations that differentiate them from domestic dogs (*SI Appendix*). Dingoes have also played cultural roles within Indigenous Australian communities. The European colonization of Australia from AD 1788 [i.e., the landing of the First Fleet (12)], however, likely had strong impacts on these long-standing ecological and cultural relationships.

Australian ecosystems were significantly altered by Europeans through land use change and the introduction of invasive species [e.g., rabbits; (13)], which have indirectly altered the diets of dingoes (14). In addition, landscape-scale dingo eradication programs, and the erection of a nationwide predator-proof fence were, and continue to be, used to protect livestock from predation by dingoes [Fig. 1*A*; (15)]. Indigenous cultural practices, including the functional and spiritual uses of dingoes (16–19), also suffered persecution throughout the colonial period. Further, the dogs introduced by European colonists in the late 18th-century were often favored by Indigenous communities due to their hunting abilities and sentinel qualities (20), which shifted the types of dogs that were present within encampments. Despite their overall morphological and behavioral differences (21, 22), dingoes retain the ability to interbreed with domestic dogs, which may have facilitated the introduction of European dog ancestry into dingo populations. In fact, some Australian-derived breeds such as the Australian Cattle Dog were developed through deliberate admixture between dingoes and European dogs (23).

Levels of European dog ancestry in dingoes have been the subject of a long-standing debate and have significant consequences for conservation. Several studies based on microsatellite assays have suggested that European ancestry is widespread among dingoes,

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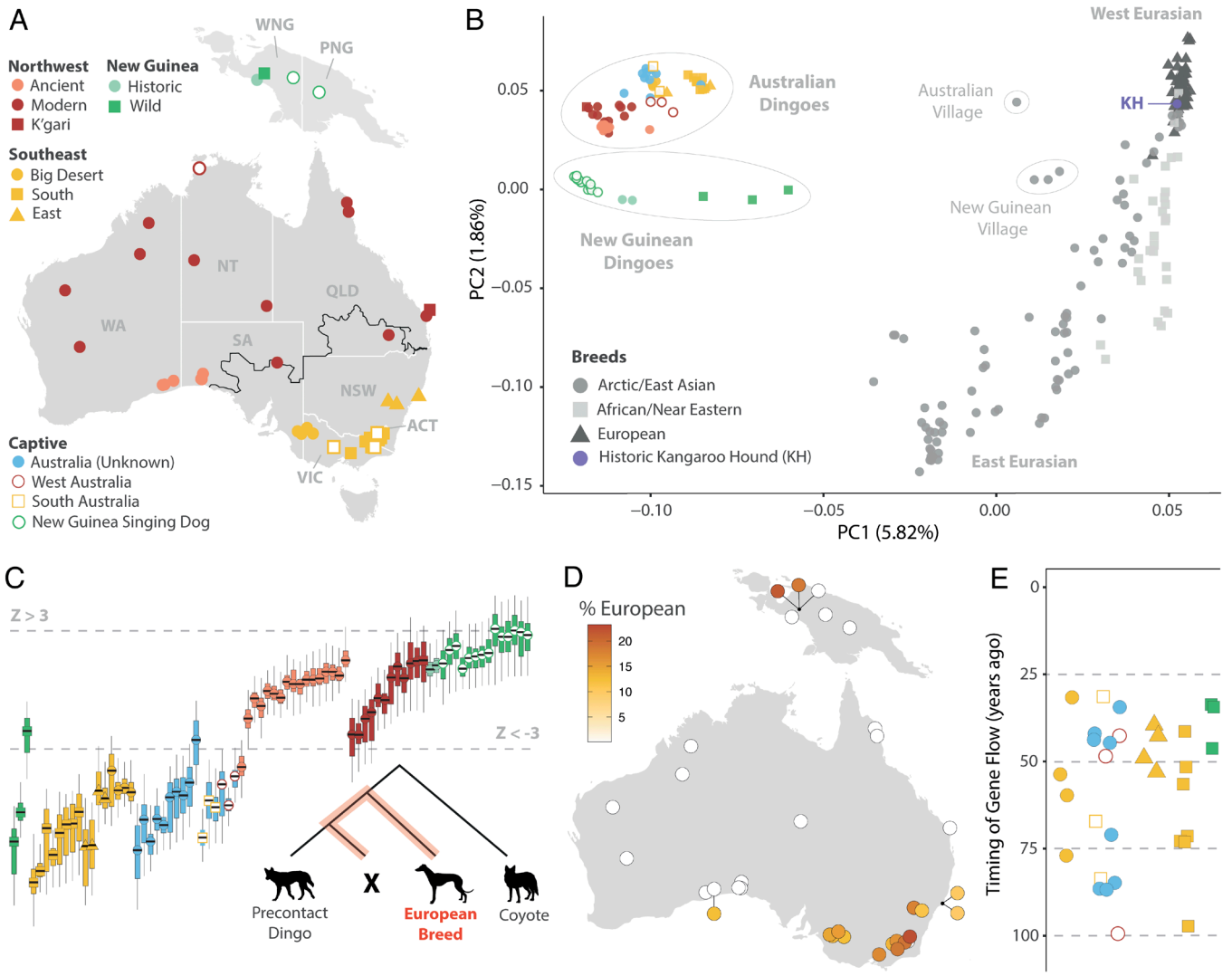

Fig. 1. (*A*) Distribution of dingoes analyzed in this study (*SI Appendix*, Table S1 *A* and *B*), highlighting the three major clades: Northwest and Southeast Australia, and New Guinea, as well as finer subclade structure (e.g., ref. 24). The extent of the Australian pest-exclusion fence, erected between 1885 and 1950, is shown (black line). State abbreviations are as follows: Australian Capital (ACT) and Northern (NT) Territories, New South Wales (NSW), Queensland (QLD), South (SA) and Western (WA) Australia (SA), Victoria (VIC), and Papua (PNG) and Western (WNG) New Guinea. (*B*) Principal components (PC) analysis of pseudohaploidized nuclear SNPs (2,720,370 transversions) from 266 individuals representing modern global dog diversity, including ancient and historic individuals from across Sahul. (*C*) Tests for gene flow between dingoes and European dogs using D-statistics of the form: D(Coyote, European Breed; X, NullarborPlain13_372), showing mean Z-scores. Significantly negative values ($Z_{mean} < -3$) indicate an excess of shared derived alleles between European breeds, and the dingo being compared. (*D*) Proportion of European ancestry (α) in dingoes calculated using F4-ratio tests, with only dingoes with statistically significant allele sharing with European breeds under D-statistic comparisons ($Z_{mean} < -3$) colored. The landing site of the First Fleet (Botany Bay) is also indicated. (*E*) Admixture timing between dingoes and European dogs estimated using exponential decay coancestry curves in MOSAIC (25). Generations were converted into years assuming the widely used 3-y generation period in dogs (26).

indicating populations are at risk of genetic dilution (27–29). In contrast, recent studies using genome-wide markers (e.g., SNP arrays) suggest that domestic dog ancestry has been overestimated, and that contemporary gene flow from dogs into dingoes is relatively uncommon (24), though such reduced-representation sequencing approaches can introduce biases (30). These estimates are also likely to have been impacted by the lack of suitable pre-colonial baselines. For instance, a recent study that included ancient dingoes identified low-level dog ancestry in several purported "pure" dingoes; however, they did not attempt to survey admixture levels in dingoes more broadly (7). To date, no studies have assessed the extent of admixture between dingoes and European dogs using exclusively whole-genome shotgun sequencing data from both ancient dingoes and a broad representative sample of present-day dingoes.

Admixture with domestic animals poses a significant threat to the genetic integrity of many wild populations (31–33). Given the distinct evolutionary trajectory of dingoes, the presence of European dog ancestry may be detrimental, yet persists at low levels given that relatively small populations cannot efficiently purify the recently admixed proportion. Alternatively, European dog ancestry may have been advantageous and spread through dingo populations, possibly due to increased genetic diversity or adaptive introgression, as observed in domestic and wild cat populations in Scotland (32), as well as in wolves (34, 35). Variation could also be neutral, and the persistence of European dog ancestry may simply be due to genetic drift.

Here, we characterized the extent, timing, and adaptive consequences of gene flow between dingoes and European dogs. We first sampled 55 directly radiocarbon dated ancient Australian

dingoes spanning the last ~2,300 y on the Nullarbor Plain (the Oondiri – Mirning and Yinyila Peoples), including both pre- (n = 31) and post-European (n = 24) periods (*SI Appendix*, Table S1*B*). We then shotgun-sequenced low-coverage (0.1 to 2.3x) nuclear genomes from 18 of these ancient Nullarbor Plain dingoes (selected to maximize temporal breadth), as well as two early 20th-century New Guinean dingoes and a mid 19th-century kangaroo hound (*SI Appendix*, Table S1*B*). To capture the extent of diversity in contemporary free-living dingo populations (since the majority of previously published genomes from Australia and New Guinea have been generated using captive individuals), we also sequenced 33 higher coverage (5.5 to 44.0x) nuclear genomes from present-day dingoes from across Australia presumed to be free from European dog ancestry (*SI Appendix*, Table S1*A*). Finally, to assess the degree to which dietary trends shifted in response to widespread colonial modification of Australian landscapes after AD 1788, we generated stable isotopic (δ^{13}C, δ^{15}N) data from all the ancient dingoes (*SI Appendix*, Table S1*B*).

Results and Discussion

West Eurasian Ancestry Detected in Post-European Contact Dingoes. To test for gene flow between European dogs and dingoes previously characterized as unadmixed (24), we first performed unsupervised ADMIXTURE analysis using five ancestral components (optimal K value based on cross-validation; *SI Appendix*, Fig. S1) on a dataset (2,720,370 transversional SNPs) containing 81 dingoes, as well as 115 purebred and 67 village dogs (*SI Appendix*, Table S1 *A–C*). These five ancestral components broadly represent major Eurasian dog lineages: Western Eurasia (i.e., Near Eastern and European), Arctic (e.g., Greenland Sled Dogs), and East Asian (36), as well as dingoes in Australia and New Guinea. Principal component (PC) analysis (Fig. 1*B* and *SI Appendix*, Fig. S2) and pairwise outgroup-f3 comparisons (*SI Appendix*, Fig. S3) showed similar differentiation between Eastern and Western Eurasian dogs, and separated Australian dingoes into two main groups: Northwest and Southeast, with captive individuals largely intermediate to both. These groups could be further separated into four regionally distinct clusters [recently described by (24)]: Big Desert, East, South, and West (which includes K'gari; *SI Appendix*, Figs. S4–S6; see *SI Appendix*).

Unsupervised ADMIXTURE analysis using two ancestral components for dingoes and exclusively European breeds suggested that Northwest Australian and both captive and historic New Guinean dingoes did not possess European ancestry, whereas Southeast and Captive Australian, and free-living New Guinean populations were estimated to possess ~12% (0 to 19.7%; *SI Appendix*, Fig. S7 and Table S2*A*). D-statistics of the form D(Coyote, European, X, Precontact Dingo) for every possible combination of dingoes (X) and European breed dogs were largely nonsignificant (i.e., the majority of $|Z| < 3$) for 17 ancient and 12 contemporary Northwest Australian dingoes. This was also true for two historical and 12 captive New Guinean dingoes, indicating little to no gene flow with European dogs (Fig. 1*C* and *SI Appendix*, Fig. S8 and Table S2*A*).

An exception was the most recent postcontact Australian dingo (mean calibrated age: AD1823; 95% CI: AD1683 to 1935), which yielded significant negative D-statistics (Z = –3.94), and ADMIXTURE results that indicated ~4% of this individual's ancestry was derived from European dogs (*SI Appendix*, Fig. S7 and Table S2*A*). European dogs (including kangaroo hounds) are known to have accompanied colonists who traversed Australia's interior and coastline, and Edward John Eyre's expedition reached the Nullarbor region as early as 1841 (37). This suggests gene flow between European dogs and dingoes may have occurred within decades of the arrival of the First Fleet. European expeditions, livestock stations, and Aboriginal trade networks could have all acted as sources of domestic dog ancestry. We also detected significant allele sharing between dingoes and the kangaroo hound (Z = –3.43), as well as an Australian Cattle Dog (*SI Appendix*, Fig. S9), supporting historical reports of intentional admixture with dingoes in the founders of these breeds (23). Is it possible that intentional mixing with dingoes may have facilitated the adaptation of kangaroo hounds and cattle dogs to the arid conditions of the Australian outback; however, our dataset lacks sufficient statistical power to test this hypothesis. In order to ascertain which dingo alleles may have been under selection, we require more data from Australian-derived European breeds.

In contrast to contemporary Northwest Australian and captive New Guinean dingoes, D-statistic comparisons for free-living populations in Southeast Australia (i.e., Big Desert, East and South) and New Guinea yielded significant negative values (Z < –3), indicating that they possess European dog ancestry (Fig. 1*C* and *SI Appendix*, Fig. S8). This signal was robust regardless of whether precontact Australian (NullarborPlain13 AD372) or historical New Guinean (NewGuineaDingo2_AD1910) dingoes were used as the unadmixed population in these tests (*SI Appendix*, Fig. S9 and Table S2*A*). Admixture fraction (calculated using F4-ratio) indicated that Captive (7.0 to 23.2%) and Southeast (9.7 to 22.5%) Australian dingoes possessed similar proportions of West Eurasian dog ancestry (*SI Appendix*, Fig. S10 and Table S2*A*). In addition, the highest levels of dog ancestry in contemporary free-living Australian dingoes coincided with regions of greater human population density, and the major sheep-grazing zone where lethal management of dingoes has been most intensive during the postcolonial period (Fig. 1*D*).

Historical, Not Recent, Gene Flow Explains the Presence of West Eurasian Dog Ancestry. The identification of widespread West Eurasian ancestry in contemporary dingo populations from Southeast Australia and New Guinea suggests gene flow with European dogs may be ongoing. Stray European dogs, however, are rare in areas outside human settlement (24). Dingoes may have instead acquired Western Eurasian ancestry primarily through episodic gene flow during the early phases of colonial settlement.

To address this question, we estimated the admixture timing between dingoes and European dogs using local ancestry inference as implemented in MOSAIC [*SI Appendix*, Figs. S11–S13; (25)], with imputed genomes of precontact Australian dingoes [exceeding 1x coverage; (38)] and European dogs used as reference populations. Mean admixture dates in Australia and New Guinea were 20.0 (95% CI: 17.5 to 22.4) and 12.7 (95% CI: 10.1 to 15.4) generations B.P., or 60 (95% CI: 53 to 67) and 38 (95% CI: 30 to 46) y ago, respectively (Fig. 1*E* and *SI Appendix*, Table S2*A*). These dates suggest that gene flow was not within the last few generations, but largely occurred during the mid 20th-century.

In Australian dingoes, this mean admixture timing is broadly coincident with the onset of aerial poison baiting in the mid-1960s that was part of widespread and intensive population management (39). This lethal control policy would not only have decreased the availability of suitable mates (40) but also disrupted social cohesion (41), thus increasing the likelihood of admixture between European dogs and dingoes. The decline in dingo populations during this time may also have been exacerbated by the ~99% reduction in rabbits linked to the spread of myxomatosis [released in the 1950s as a biological control method; (42)], which form a key component of the diet of dingoes (14). Patterns of introgression between introduced and local populations associated with

dramatic population declines (despite centuries of overlap) have been demonstrated in other species including the Scottish wildcat (32, 43). Our analysis indicates that gene flow into highland New Guinean dingoes likely occurred more recently, potentially due to their isolation at high altitudes until the construction of settlements and roads associated with the development of large-scale mineral mines in the late 1980s, such as the Grasberg Gold Mine (3, 44).

These differences in admixture timing, alongside the distinct colonization histories of Australia and New Guinea, suggest that West Eurasian ancestry may have been introduced by different dog populations. To determine the closest source for each individual, we extracted the ancestry blocks assigned as "European" by MOSAIC and calculated outgroup-f3 statistics for comparisons against all modern breeds (*SI Appendix*, Fig. S14). West Eurasian ancestry in Australian dingoes was a close match to the types of dogs that have been common in Australia since European arrival (45), such as hounds, retrievers, and spaniels (*SI Appendix*, Table S2*B*). In New Guinea; however, West Eurasian ancestry showed the strongest affinities toward Southeast Asian breeds (*SI Appendix*, Table S2*B*), which possess both East and West Eurasian ancestry (46). This supports ethnographic reports that suggest New Guinean dingoes interbred with local village dogs (47), rather than European breed dogs as in Australia.

Genomic Health of Dingoes Influenced by Recent Gene Flow. The persecution of Australian dingoes since European colonization has potentially reduced their genetic diversity. To test this, we estimated the number and length of runs of homozygosity (ROH) in dingoes, as well as 184 modern dog breeds, and village dog populations across island Southeast Asia and Africa. Dingoes possessed an excess in both the total number and length of the genome in ROH relative to all other dogs, including breed dogs (Fig. 2*A* and *SI Appendix*, Fig. S15). The inbreeding coefficient measured as F_{ROH} (the proportion of the total genome in ROH) ranged between 44 to 85% in contemporary free-living Australian dingoes, the lowest of which were higher than 95% of all village dog populations (F_{ROH}: 6 to 21%), and over 80% of modern breeds tested (F_{ROH}: 11 to 69%; *SI Appendix*, Table S2*C*).

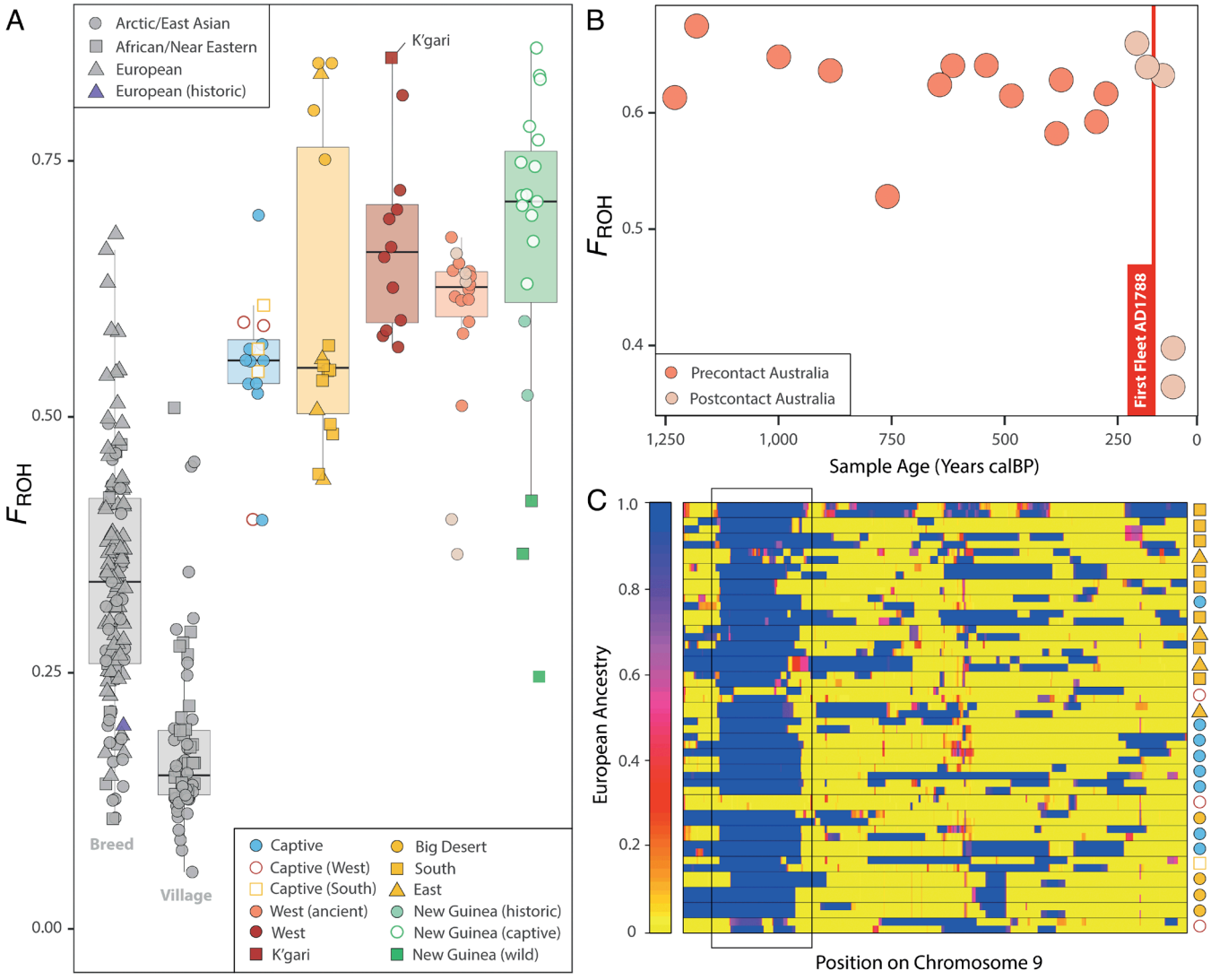

Fig. 2. (*A*) Boxplots of F_{ROH} for dingo clades, namely captive, Southeast, and Northwest (both modern and ancient) Australian and New Guinea, with breed and village dogs for comparison. (*B*) F_{ROH} estimates in Southwest Australian (Nullarbor Plain) dingoes through time, indicating the arrival of the First Fleet (AD1788). (*C*) Distribution of European dog ancestry (colored based on assignment probability) along chromosome 9 [inferred using MOSAIC; (25)] for Southeast and captive Australian dingoes, highlighting a ~16 Mb region with significant excess of European alleles (see also *SI Appendix*, Fig. S19). Individuals are ordered based on the genome-wide proportion of West Eurasian ancestry.

Big Desert dingoes showed the highest levels of inbreeding (F_{ROH}: 75 to 85%), despite also possessing West Eurasian ancestry. They also showed an excess of moderate (1 to 2 Mb: 15.1%) and long (>2 Mb: 17.9%) ROH relative to all other dogs (*SI Appendix*, Fig. S16). This likely reflects population declines driven by historical and ongoing lethal control. Current census data suggest that there may be fewer than 40 living adult dingoes from this population remaining (48). Moderate (16.5%) and long (9.9%) ROH were also elevated in the K'gari dingoes (F_{ROH}: 85%; *SI Appendix*, Fig. S16), which has likely been driven by founder effects [i.e., precolonial translocation of a small number of dingoes to the island by the Butchulla People (49)], sustained low population size [70 to 200 individuals; (50, 51)], and recent bottlenecks resulting from culling (52).

In contrast, fewer ROH segments were identified in free-living New Guinean dingoes (F_{ROH}: 25 to 42%) relative to historical (F_{ROH}: 52 to 59%) and highly inbred captive (F_{ROH}: 63 to 86%) populations. A similar pattern is also evident in South and East (F_{ROH}: 44 to 84%) Australian dingoes relative to those in the Northwest (F_{ROH}: 57 to 81%; Fig. 2*A*). These F_{ROH} reductions are the result of introgressed West Eurasian ancestry disrupting autozygous segments. To directly assess whether gene flow led to an increase in genomic diversity, we compared heterozygosity estimates both within and outside regions of West Eurasian ancestry. We found heterozygosity to be significantly higher within introgressed blocks for almost all individuals (t = 3.403, *P*-value = 0.001), with an excess of ~12% on average compared to genome-wide diversity (*SI Appendix*, Fig. S17).

Levels of inbreeding in isolated Southwest Australian (Nullarbor Plain) dingoes remained relatively stable for at least 1,000 y before the arrival of the First Fleet in AD 1788 (F_{ROH}: 51 to 68%). This suggests that low diversity in contemporary dingo populations is the result of founder effects and long-term demographic history, rather than a recent population decline. Postcolonial Southwest Australian dingoes, however, show reduced F_{ROH} (F_{ROH}: 37 to 66%; Fig. 2*B*) due to gene flow from European dogs. In contrast, contemporary Northwest Australian dingoes showed levels of inbreeding consistent with precontact dingoes (F_{ROH}: 57 to 81%). This discrepancy suggests that unlike dingoes in Southeast Australia, European ancestry did not persist in Northwest Australian populations, likely due to lower density of dogs and less effective lethal control programs in this region of Australia (53).

We also identified an uneven distribution of ROHs across the genome (*SI Appendix*, Fig. S18). While many of these ROH "islands" and "deserts" were shared between Australian and New Guinean dingoes, potentially as a result of selection, others were lineage specific. In Australian dingoes, for instance, we identified a region of high autozygosity on chromosome nine which overlapped a ~16 Mb region that possessed an excess of West Eurasian ancestry (7,401,897 to 23,194,765; Fig. 3*C* and *SI Appendix*, Fig. S19) and exhibited elevated *Fst* levels in comparisons between precontact Southwest and contemporary dingoes across Australia (*SI Appendix*, Fig. S20 and Table S2*D*). Within this ~16 Mb region, 24 individuals were homozygous for West Eurasian ancestry. Our analyses indicate that the high frequency of this European haplotype (~85%) in contemporary dingoes is unlikely to be explained by drift alone (Fig. 2*C* and *SI Appendix*, Fig. S19). Coalescence patterns within this genomic block indicate that dingoes which possess European haplotypes formed multiple paraphyletic clades, although the majority clustered within a single clade that also included the kangaroo hound (*SI Appendix*, Fig. S21). Combined, these patterns indicate that this European haplotype was likely acquired through multiple events of gene flow with European dogs, and rose in frequency in dingoes due to positive selection. We could not determine which of the 394 protein-coding genes within this region (*SI Appendix*, Table S2*E*) were under selection, however, since the entire region exhibited elevated *Fst* (between precontact and contemporary dingoes; *SI Appendix*, Fig. S20) due to the recency of gene flow. In addition, even if the candidate gene regions could be identified, we could not ascertain which haplotype is under selection.

Dietary Shifts Influenced by European Colonization. Europeans likely also impacted dingoes indirectly by altering the Australian landscape. While previous studies have characterized regional differences in diet through direct identification of prey species in fecal and stomach contents (14), these techniques have been limited to contemporary populations. To test for potential shifts in dingo diet through time, we measured carbon ($\delta^{13}C$) and nitrogen isotope ($\delta^{15}N$) values in collagen from 55 directly dated dingoes from the Nullarbor Plain in Southwest Australia (*SI Appendix*, Table S1*B*). We focused exclusively on the Nullarbor Plain dingoes to avoid confounding our analysis with local differences in environment (e.g., diversity of prey species, climate regimes, vegetation). The relative proportions of carbon isotopes ($^{13}C/^{12}C$) indicate whether an organism's diet is dominated by C_3 (low $\delta^{13}C$) or C_4 (high $\delta^{13}C$) plants, whereas nitrogen isotopes ($^{15}N/^{14}N$) are indicative of trophic level (organisms that are lower in the food chain possess low $\delta^{15}N$ values). Our dataset represented 31 precontact (before AD 1788) and 24 postcontact dingoes (*SI Appendix*, Figs. S22 and S23), with the earliest individual dated to 2358 to 2331 calibrated years B.P. (calBP; OxA-42512: 2326 ± 19 B.P.).

Over the last two millennia, dingoes in Southwest Australia possessed a range of relatively high $\delta^{13}C$ (−19.3‰ to −12.2‰) and $\delta^{15}N$ (12.5‰ to 18.6‰) values, consistent with high trophic level predators in arid environments (Fig. 3*A* and *SI Appendix*, Fig. S24). We found a significant decrease in both $\delta^{13}C$ (t = −2.2579, *P*-value = 0.028) and $\delta^{15}N$ (t = −2.0997, *P*-value = 0.041) values after AD1788 (Fig. 3*B*). This pattern is true of individuals recovered at the same site. These shifts likely reflect multiple drivers including changes in vegetation and prey availability due to changes in land management, and the introduction of non-native animals.

Although rabbits comprise a large portion of the diet of dingoes in arid and semiarid zones today (14), they only became invasive after AD1859 (13). Conversely, cats had established feral populations across Australia by at least the 1840s (54) and are implicated in the decline and extinction of many native species, particularly small mammals (55). The lower trophic level of postcontact dingoes may therefore reflect a dietary shift from small native omnivores (e.g., bandicoots) and carnivores (e.g., dasyurids) to larger native herbivores (e.g., kangaroos and emus), due to direct competition with feral cat populations (55).

Alternatively, given that these shifts occurred during a period of relatively stable climate, prey abundance may have also been influenced by changes in vegetation, driven by the cessation of traditional land management [e.g., altered fire regimes; (56)] and/or the spread of pastoralism (56). Land leases for sheep and cattle grazing on the Nullarbor Plain were first granted in the late 19th-century (57). It is therefore possible that earlier, extensive landscape clearing, alterations to local hydrology, and intensive livestock grazing in eastern Australia may have exacerbated aridification across the country (58).

Conclusions. Our results illustrate how European colonization, through the introduction of dogs, invasive species, and land use changes, impacted both the ancestry and ecology of dingoes. Recent studies have suggested that present-day gene flow between dingoes and European dogs is uncommon (24). Our study,

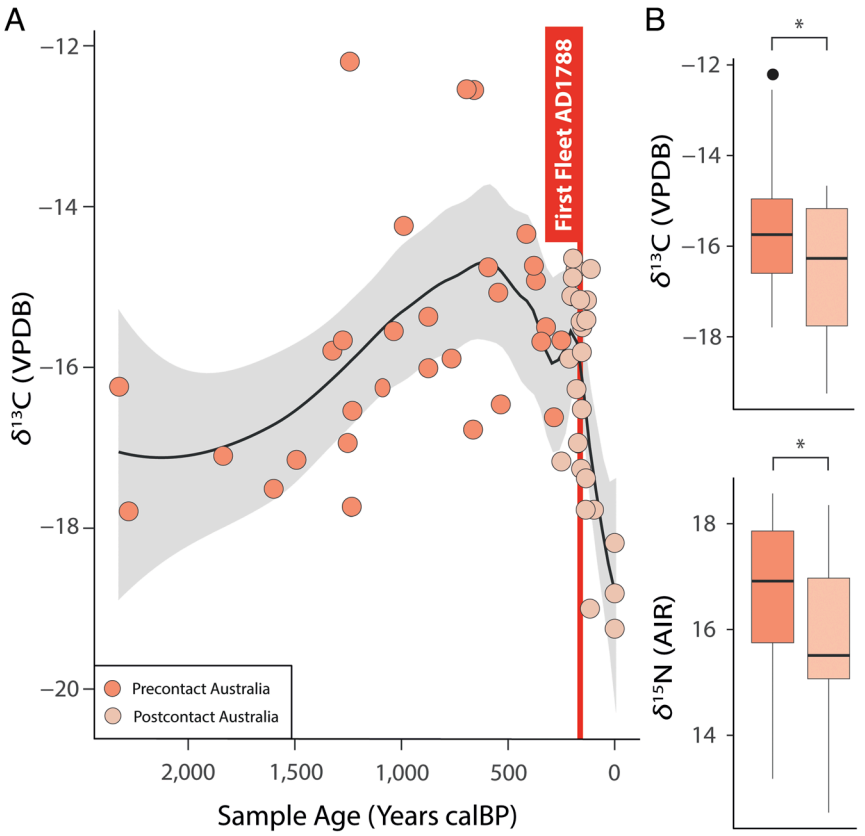

Fig. 3. (*A*) Temporal shifts in δ^{13}C values (*SI Appendix*, Table S1*B*) from ancient dingoes on the Nullarbor Plain (Southwest Australia) over the last two millennia, highlighting the arrival of European colonists onboard the First Fleet (AD1788). (*B*) Mean differences in δ^{13}C (*Top*) and δ^{15}N (*Bottom*) values between pre- and postcontact dingoes. Both comparisons are statistically significant (*$P < 0.05$).

which analyses a time series of shotgun-sequenced genomes that spanned both the pre- and postcontact periods, as well as a broader geographic representation of contemporary dingo populations, instead reveals evidence for widespread interbreeding across Australia prior to the 21st-century. This European dog ancestry, however, is not homogeneously distributed across populations of Australian dingoes, but is instead concentrated in areas with the highest human land use intensity.

While European dog ancestry in dingoes is often considered negative, there may be unappreciated benefits, similar to those documented in other canids [e.g., wolves; (34, 35)]. Inbreeding in dingoes appears to be largely associated with their establishment in and across Australia over 3,000 y ago, although it has been exacerbated by postcolonial persecution. In some populations that experienced severe bottlenecks, our results show that European ancestry from historical admixture has increased heterozygosity, potentially mediating the effect of recent inbreeding. We also found evidence that some genomic regions of European ancestry introduced by historical admixture that persist in present-day dingoes may be adaptive. Given the widespread changes that European colonization induced in Australian ecosystems, and the fact that European dogs likely introduced new diseases, it is possible that some European ancestry may have proven beneficial to dingoes.

Our study adds to a growing body of evidence that suggests gene flow with European dogs has done little to compromise the health or distinctiveness of dingo populations across Australia (7, 24, 59). Admixture appears to only present a threat when coupled with human interventions aimed at reducing the population sizes of dingoes, which disrupt their social cohesion, and may weaken the ability of selection to regulate European dog ancestry. To preserve long-term, viable, and ecologically functional populations of dingoes, management strategies should focus on maintaining large enough populations in which natural selection, either positive or negative, rather than drift, can purge, or increase the frequency of European haplotypes that influence individual fitness. Given this, policy makers in Australia should consider a flexible framework that maintains the distinctiveness of dingoes, while acknowledging that European ancestry persists in many populations from historical (i.e., mid 20th-century) admixture (60).

Dingoes are just one example of a free-living animal population affected by postcolonial gene flow. The introduction of modern chicken breeds into peninsular Southeast Asia, for example, likely affected the ancestry of wild jungle fowl (31), and postconquest changes in agriculture and traditional management practices led to hybridization between South American camelids [i.e., llama and alpaca; (61, 62)]. Although precontact dingoes from the Nullarbor Plain are unlikely to be representative of the entire precolonial diversity across Australia, they have not been influenced by historical gene flow with European dogs – a factor that has undermined confidence in the conclusions of previous studies (24, 27, 28, 63, 64). Our results suggest that in order to assess the complex histories of admixture associated with the global spread of Europeans and the introduction of their domesticates, it is essential to establish ecological and genomic baselines for precolonial populations.

Materials and Methods

For detailed descriptions of sample acquisition, data generation, and analytical protocols, see *SI Appendix*. Blood, saliva, or tissue samples were collected from 33 contemporary dingoes from across Australia (Fig. 1*A* and *SI Appendix*, Table S1*A*) and sent to the National Institute of Health's Intramural Sequencing Center (MD, USA) for whole-genome sequencing. We selected these individuals as they were

assessed to be "free" of contemporary domestic dog ancestry based on Axiom Canine HD Genotyping (24), which enabled us to test whether the combination of whole-genome sequencing, and the inclusion of precolonial baselines, would lead to more accurate characterization of admixture. For ancient (i.e., recovered from pitfall cave deposits) Australian dingoes, petrosal bones and teeth were sampled from 55 individuals from across the central Nullarbor Plain. We also sampled petrosal bones from two historical (i.e., sourced from museum collections) New Guinean dingoes collected during the British Ornithologists Union expedition in 1910 along the Mimika River, and a kangaroo hound (AD1843), housed at the Natural History Museum in London (NHMUK; *SI Appendix*, Table S1*B*). Ultrapurified collagen was isolated from all ancient Australian dingoes and submitted for both AMS dating at the Oxford Radiocarbon Accelerator Unit (*SI Appendix*, Figs. S22 and S23), and stable isotope ($\delta^{13}C$, $\delta^{15}N$) analysis (*SI Appendix*, Fig. S24) at the Research Laboratory for Archaeology and the History of Art (University of Oxford).

Ancient DNA from the 55 nonmodern (i.e., historical and ancient) samples was extracted as per published methods (65) at the University of Oxford's Palaeogenomics and Bioarchaeology Research Network, or as previously reported (7). All subsequent lab work and bioinformatic analyses were carried out at the University of Oxford. Extracts were converted into double-stranded DNA libraries (66) and dual-indexed using 6 bp barcodes (67). Purified libraries were pooled and screened on either an Illumina HiSeq X Series at Macrogen (Seoul, South Korea) or an Illumina NextSeq 1000 at Genzentrum (Munich, Germany), using 150 bp and 60 bp paired-end sequencing chemistry, respectively. Reads were processed using AdapterRemoval v.2.3.3 (68), with collapsed reads mapped to the CanFam3.1 reference assembly (26) using *bwa aln* v.0.7.17-r1188 (69), PCR duplicates removed with samtools v.1.9 (70), and ancient DNA authenticated with MapDamage [*SI Appendix*, Fig. S25; (71)].

Based on the proportion of endogenous DNA and mean calibrated age for each sample, we selected a time series of 18 ancient Australian dingoes, as well as the three historical individuals, for whole-genome sequencing (*SI Appendix*, Fig. S26). Reads were processed using nf-core/eager v.2.4.6 (72), and samtools was used to calculate mean depth and breadth of coverage, and perform read-based genetic sex determination. We then used bcftools v.1.9 (73) to merge our nonmodern (n = 21) and modern (n = 33) genomes with publicly available genomes of purebred (n = 115) and village (n = 67) dogs, Australian (n = 11) and New Guinean (n = 17) dingoes, and a coyote for a final dataset of 266 canids (*SI Appendix*, Table S1*C*). We chose not to include recently published SNP-capture data from ancient Southeastern Australian dingoes [e.g., Curracurrang; (7)] due to possible downstream biases (30). To minimize biases due to differential coverage and DNA damage in nonmodern samples, we filtered for transversional SNPs, excluding sites with low minor allele frequency (>1%), and those under strong linkage disequilibrium ($R^2 > 0.5$), resulting in 2,720,370 variants.

Principal Components analysis was performed in *smartpca* (74) on both the complete pseudohaploid dataset, as well as a subset containing exclusively Australian dingoes. We then computed distance matrices using 1) all possible outgroup-f3 comparisons using the *Calc-f3* function in struct-f4 (75), and 2) an identity by state matrix, which we used to construct a neighbor-joining tree in the R package *ape* v.5.4.1 (76). We also constructed a maximum-likelihood phylogeny in IQ-TREE v.2.1.4 (77) using 33 modern and 18 high-coverage (7.7 to 276.2x) nonmodern mitochondrial genomes, alongside 165 publicly available sequences spanning the last ~13,000 y (*SI Appendix*, Table S1*D*). To test for gene flow between European dog breeds (X) and dingoes (Y), we used both ADMIXTURE v.1.3.0 (78), and D-statistics of the form: D(Coyote, X; Y, NullarborPlain13_372) and D(Coyote, NullarborPlain13_372; X, Australian breed), with ancestry proportions calculated using F4-ratio estimation (79).

Nonmodern genomes were then imputed in GLIMPSE v1.1.1 (80) following published methods (38), resulting in 6,611,861 autosomal variants (both transitions and transversions), a subset (--thin 1,000) of which (1,435,742 variants) were used to estimate genome-wide local ancestry and admixture timing in MOSAIC v.1.5.0 (25). European ancestry blocks were then extracted and used to both determine the closest modern breed match [following the functional designations of (81, 82)] through outgroup-f3 comparisons, and calculate heterozygosity in introgressed regions. We also calculated runs of homozygosity in PLINK v.1.90b6.21 following established methods (83), which were used to estimate both the fraction of each individual's genome in ROH (F_{ROH}), and the frequency distribution of autozygous segments across Australian and New Guinean populations (e.g., ref. 84).

Finally, we performed a sliding window Fst scan (85) in vcftools to detect differences between pre- and postcontact imputed dingoes, checking for overlap with regions of excess European ancestry. We then used BEDTools *intersect* v2.30.0 (86) and the CanFam3.1 annotation to identify genes within these regions. We also used HAYSTAC (87) to assess differences in microbial diversity between pre- and postcontact dingoes, comparing each individual against prokaryotic and viral databases (*SI Appendix*).

Data, Materials, and Software Availability. All newly generated modern sequences (SAMN43506323–SAMN43506355) used in this study are stored in the European Nucleotide Archive (ENA) under BioProject PRJNA1157190 (https://www.ebi.ac.uk/ena/browser/view/PRJNA1157190) (88). All newly generated ancient sequences (SAMEA117852278–SAMEA117852298 and SAMEA117854780–SAMEA117854816) are available in the ENA under BioProject PRJEB73844 (https://www.ebi.ac.uk/ena/browser/view/PRJEB87437) (89). All other data are included in the manuscript and/or supporting information.

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