

What is a dingo – origins, hybridisation and identity

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ABSTRACT

Controversy about the nomenclature and taxonomy of dingoes has sparked interest in their complex identity. At the root of taxonomy debates are differences in the species concepts employed, differing opinions about the domestication status of dingoes (and their ancestors) and a simplistic handling of the complex evolutionary relationship between wolves, dingoes and domestic dogs. I explore the relationship of dingoes to village dogs, modern breed dogs and wolves using genome-wide SNP data and discuss the implications of these findings to the ongoing debate about dingo identity and nomenclature. Importantly, despite controversy about what to call dingoes and whether they are a full species, these animals represent an important, distinct and unique evolutionary unit worthy of high conservation priority, as a native species. There is growing concern about the spread of domestic dog genes into dingo populations, particularly in southeastern Australia, and the impact this has on conservation goals. However, the discovery of biogeographic subdivision within dingoes raises questions about the accuracy of the current methods used for estimating dog vs dingo ancestry. I caution scientists and wildlife managers to carefully consider the limitations of current ancestry estimate methods when assessing DNA test results. Future work using genome-wide DNA technology to improve dingo ancestry estimates will be fundamental to ongoing debate about what dingoes are, how to identify dingoes and how to conserve them.

Key words: Dingo, Dog, domestication, hybridisation, evolution, *Canis dingo*, *Canis familiaris*, nomenclature

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Introduction

The dingo is a controversial animal and experts widely debate how to manage them, how to conserve them, how they arrived in Australia, when they arrived in Australia and where their ancestors originated. Recently there has been ongoing discussion concerning the most appropriate nomenclature and taxonomic classification for dingoes; *Canis familiaris* (Jackson *et al.* 2017; Jackson *et al.* 2019) or *Canis dingo* (Smith *et al.* 2019). At the root of these debates are differences in the species concepts employed, different opinions about the evolutionary relationship between dogs, dingoes and wolves and a simplistic view of the domestication status of dingoes and primitive dogs. Despite these different opinions about nomenclature, scientists agree that dingoes represent a native animal with high conservation priority for their ecological, cultural and evolutionary identity. Here I use existing data from genome-wide SNPs to further explore the relationship of dingoes to global populations of village dogs, domestic dog breeds and wolves. In particular, I interrogate the question of whether dingoes fall 'within' the same phylogenetic grouping as domestic dogs. Based on these analyses I discuss hypotheses about the role of domestication in the evolution of the dog and the taxonomy of dog lineages. Finally, I explore the identity of dingoes within Australia in the context of conservation management,

considering how knowledge about hybridisation and genetic subdivision should be shaping conservation and management strategies.

The process of domestication

Domestication is a complex, prolonged and multi-stage process. Larson and Burger (2013) describe the following stages in the domestication pipeline: "anthropophily, commensalism, control in the wild, control of captive animals, extensive breeding, intensive breeding, and finally to pets/livestock". Most extant dog populations have been strongly shaped by domestication and humans (Pilot *et al.* 2015) and, whilst there are free-breeding extant dog populations these are often reliant upon anthropogenic sources of food and water and have poor success in rearing offspring with high juvenile mortality, these dogs are feral rather than wild living (Boitani and Ciucci 1995; Boitani *et al.* 1995; Boitani *et al.* 2006; Atickem *et al.* 2010). To date the only known occurrence of a truly feral western dog population was on the Galapagos Islands (Reponen *et al.* 2014). This population persisted for ~150 years before it was eradicated in the 1980s and the population has not re-established despite extensive stray and free-breeding dog populations around towns (Barnett 1986; Reponen *et al.* 2014). The success of this feral population was perhaps

related to the unique conditions of the Galapagos which lacks native predators and thus has naive prey populations (Barnett 1986). The rarity of true feral dog populations despite the widespread occurrence of dogs globally, suggests that domestic dogs have been altered to the extent that they are largely unable to successfully persist in the wild. In Australia, DNA testing corroborates that feral domestic dogs have poor survival in the wild and represent less than 1% of the wild canine population (Stephens *et al.* 2015; Cairns *et al.* 2019). However, hybridisation is considered a serious issue because of the widespread occurrence of domestic dog ancestry in dingoes from southeastern Australia (Stephens *et al.* 2015; Cairns *et al.* 2019).

Evolutionary history of dogs through time

Dogs are an enigmatic species sharing a close relationship with humans and were the first species to be domesticated (Manwell and Baker 1984; Larson *et al.* 2012; Freedman and Wayne 2017). However, there is still much to unravel regarding the evolution of the canis species complex (Gopalakrishnan *et al.* 2018). Indeed, the evolutionary history of canis species is complicated because of historical admixture between jackal, coyote, wolf and dog lineages (vonHoldt *et al.* 2011; Fan *et al.* 2015; Freedman and Wayne 2017; Gopalakrishnan *et al.* 2018; Schweizer *et al.* 2018; Wang *et al.* 2019). Molecular dating suggests that the first dogs evolved approximately 20,000-40,000 years BP (Pang *et al.* 2009; Druzhkova *et al.* 2013; Thalmann *et al.* 2013; Freedman *et al.* 2014; Skoglund *et al.* 2015; Freedman and Wayne 2017; Oetjens *et al.* 2018). Archaeological estimates of the divergence time between wolves and dogs is approximately 15,000-36,000 years BP (Germonpre *et al.* 2009; Germonpre *et al.* 2012; Larson *et al.* 2012; Skoglund *et al.* 2015; Frantz *et al.* 2016; Freedman and Wayne 2017). It is not clear which wolf population is the direct ancestor of dogs, and the current working hypothesis is that dogs evolved from a now extinct Pleistocene wolf rather than any of the modern wolves (Thalmann *et al.* 2013; Freedman *et al.* 2014; Fan *et al.* 2015; Freedman and Wayne 2017). Practically this means that whilst modern wolves are the closest relatives of dogs they are may not be the direct ancestor of dogs (Freedman and Wayne 2017).

Some authors have posited that dogs arose as a natural species before being domesticated by humans (Koler-Matznick 2002; Koler-Matznick 2016). There is also continued debate concerning where the first dogs (or proto-dog) arose (Pang *et al.* 2009; Thalmann *et al.* 2013; Freedman *et al.* 2014; Pilot *et al.* 2015; Shannon *et al.* 2015; Skoglund *et al.* 2015; Frantz *et al.* 2016; Wang *et al.* 2016; Ní Leathlobhair *et al.* 2018). Genetic studies have observed that admixture with different wolf populations may have facilitated diversification in dogs (Sacks *et al.* 2013; Freedman *et al.* 2014; Fan *et al.* 2015; Skoglund *et al.* 2015). As suggested by Freedman and Wayne (2017) likely the first proto-dogs arose ~25,000 years BP living an anthropophilic lifestyle around humans. Whether the

proto-dog was domesticated depends on the definition of domestication which is used, and particularly whether anthropophilic or commensal animals are considered to be “domesticated”. These first proto-dogs may have begun to associate more closely with humans in a commensal and/or mutualistic relationship. This was followed by at least one period of intensive selection (domestication) as human cultures moved to a sedentary lifestyle during the rise of agriculture approximately 10,000 years BP (Axelsson *et al.* 2013; Arendt *et al.* 2016; Freedman *et al.* 2016; Pendleton *et al.* 2018) and another period of intensive selection during the formation of domestic dog breeds in the Victoria era (vonHoldt *et al.* 2010; Parker 2012; Freedman *et al.* 2016; Parker *et al.* 2017; Pendleton *et al.* 2018).

There is empirical evidence of at least three major clades or lineages of dog: East Asian dogs (Pang *et al.* 2009; Freedman *et al.* 2014; Pilot *et al.* 2015; Frantz *et al.* 2016; Wang *et al.* 2016), Pre-Contact dogs (Brown *et al.* 2013; Brown *et al.* 2015; Ní Leathlobhair *et al.* 2018) and Eurasian domestic dogs (vonHoldt *et al.* 2010; Freedman *et al.* 2014; Pilot *et al.* 2015; Shannon *et al.* 2015; Parker *et al.* 2017). The evolutionary history of these different dog lineages is complicated because of the mobility of dogs across the world throughout history leading to the swamping or extinction of some Pre-Contact or East Asian dog lineages by modern Eurasian dogs (Brown *et al.* 2013; Brown *et al.* 2015; Pilot *et al.* 2015; Wang *et al.* 2016; Ní Leathlobhair *et al.* 2018). East Asian dogs are a basal (ancient) lineage, hypothesized to have diverged from other dogs approximately 10,000-20,000 years ago and have been the origin of several waves of dog admixture into Eurasia and the Western world over the Anthropocene (Pang *et al.* 2009; Freedman *et al.* 2014; Pilot *et al.* 2015; Wang *et al.* 2016).

Evolutionary origins of dingoes

Our knowledge about the origins of dingoes has been shaped by anthropology, archaeology, morphology and genetics. Anthropology indicates that dingoes have coexisted with humans in Australia for thousands of years, with dingoes featuring heavily in rock art and oral history kept by the First people of Australia (Smith and Litchfield 2009; Smith 2015; Fillios and Taçon 2016). Dating of dingo archaeological remains suggest that they arrived in Australia at least 3,500 years BP (Macintosh 1964; Gollan 1984; Balme *et al.* 2018) but it is not clear how they arrived in Australia (Fillios and Taçon 2016). The oldest archaeological deposits of dog remains in southeast Asia have been dated at approximately 3,000-4,000 years BP (Gonzalez *et al.* 2013; Piper *et al.* 2014; Greig *et al.* 2015; Fillios and Taçon 2016; Jones *et al.* 2019).

There are strong morphological similarities between dingoes and Asian dogs, for example the village dogs of Thailand, Vietnam and Borneo (Corbett 2001b). Mitochondrial and Y-chromosome studies identify close relationships between dingoes, New Guinea Singing Dogs

(NGSD) and Asian village dogs (Savolainen *et al.* 2004; Oskarsson *et al.* 2011; Ardalan *et al.* 2012; Sacks *et al.* 2013; Cairns and Wilton 2016; Cairns *et al.* 2017), indicating that the ancestor of dingoes was likely of East Asian origin. vonHoldt *et al.* (2010) used genome-wide SNP data to model the relationships of various domestic dog breeds, dingoes and wolves, they observed that dingoes cluster with 'primitive' breeds such as the Basenji, Sharpei and Chow Chow. A key clue to the identity of dingoes is their lack of AMY2B duplication, which is widely observed in extant domestic dog populations and considered to be a key feature of dog lineages associated with agriculture (Axelsson *et al.* 2013; Freedman *et al.* 2014; Arendt *et al.* 2016). This is evidence that dingoes likely diverged from the dog phylogeny prior the rise of agriculture and thus the intensive domestication of dogs. However, there is ongoing debate concerning whether dingoes represent a feral domestic dog or a remnant proto-dog (Jackson *et al.* 2017; Ballard and Wilson 2019; Jackson *et al.* 2019; Smith *et al.* 2019).

Proto-dog or domestic dog?

The dingo is unique to Australia, occurring across the mainland continent and K'Gari (Fraser Island) but not Tasmania. Ballard and Wilson (2019) suggest that there is little evidence that dingoes are a feral domesticate. Crowther *et al.* (2014) show that dingoes form a discrete taxon distinguishable from domestic dogs, wolves and other canids. A review of morphological, behavioural, ecological, biological and genetic evidence by Smith *et al.* (2019) posits that dingoes represent a remnant proto-dog lineage distinct from both wolves and domestic dogs, but perhaps intermediate between wolves and domestic dogs. For example, dingoes exhibit a single seasonal breeding period (Lord *et al.* 2013; Smith 2015; Cursino *et al.* 2017) compared to domestic dogs that are generally capable of breeding twice a year (Engle 1946; Boitani *et al.* 2006). Wild canids such as wolves, coyotes, red wolves and jackals possess social monogamy with allopatric parental care (Macdonald *et al.* 2019) which is also observed in dingoes (Lord *et al.* 2013; Smith 2015) but not domestic dogs. Morphologically dingoes have larger carnassial and canine teeth, larger auditory bullae (Newsome *et al.* 1980; Newsome and Corbett 1982; Corbett 2001b), a flatter cranium, larger nuchal and sagittal crests (Newsome *et al.* 1980; Newsome and Corbett 1982; Jones 1990; Geiger *et al.* 2017), a longer muzzle (Newsome *et al.* 1980; Newsome and Corbett 1982), and a larger brain/body size (Smith *et al.* 2017), compared to domestic dogs. Genetic evidence also observes dingoes as a diagnosable and distinct, if phylogenetically closely related, lineage of canid which is geographically isolated to Oceania (Cairns *et al.* 2018; Smith *et al.* 2019). The alternate position posited by Jackson *et al.* (2017 and 2019) is that dingoes are an evolutionary lineage indistinguishable from domestic dogs and should therefore be considered a breed or variety of *Canis familiaris*. This position is based on the hypothesis that all dogs were formed through direct domestication of the wolf (*Canis lupus*) by humans.

The modern identity of dingoes – population subdivision and hybridisation

A central issue to the conservation of dingoes is the presence of domestic dog hybridisation and the question of whether dingoes form a single homogenous population or several ecotypes. Hybridisation has been identified to exist in dingo populations based on skull morphometrics (Newsome *et al.* 1980; Newsome and Corbett 1982; Jones 1990; Woodall *et al.* 1996; Corbett 2001b; Elledge *et al.* 2008; Jones 2009) and microsatellite DNA testing (Wilton 2001; Elledge *et al.* 2008; Stephens *et al.* 2015; Cairns *et al.* 2019). Geometric morphometrics of dingoes and hybrids suggest that cranial morphology is highly conserved and so hybrids cannot be reliably distinguished from pure dingoes based on skull morphology alone (Parr *et al.* 2016). The incidence of hybridisation is reported to be higher in southeastern Australia leaving some scientists to fear that dingoes will be driven to extinction through genetic dilution (Daniels and Corbett 2003; Jones 2009; Glen 2010; Claridge *et al.* 2014; Stephens *et al.* 2015). Originally it was believed that dingoes formed a single population, possibly derived from a single pregnant female being brought to Australian shores (Savolainen *et al.* 2004; Oskarsson *et al.* 2011). However, genetic studies of mitochondrial (Cairns and Wilton 2016), Y-chromosome (Sacks *et al.* 2013; Cairns *et al.* 2017) and genome-wide (Cairns *et al.* 2018) markers have identified several different lineages of dingo: southeastern, northwestern and K'Gari (Fraser Island). Studies based on 3D cranial morphology have also identified evidence of ancient population substructure in dingoes (Koungoulos 2020).

Analysis of genome-wide data and results

I carried out detailed analyses of genome-wide single nucleotide polymorphism (SNP) data using published data from Vaysse *et al.* (2011), Shannon *et al.* (2015) and Cairns *et al.* (2018) to explore the evolutionary history of dingoes compared to free-breeding village dogs, breed dogs and some wolves from across the world. All dingoes were estimated to be pure dingoes according to microsatellite testing and were representative of five geographic regions across Australia: the Kimberley, the Gibson Desert, the Simpson Desert, K'Gari (Fraser Island) and the Australian Alpine Region (Cairns *et al.* 2018). The data collected by Vaysse *et al.* (2011) and Shannon *et al.* (2015) includes representatives of many domestic dog breeds and village dog populations from across the world. A set of 14 wolf samples are included in these analyses from North America, the Middle East and Israel (Vaysse *et al.* 2011). The samples in these datasets were all genotyped on Illumina Canine HD170K microarrays. Full methodological details are provided in the SI Appendix.

Principal components analysis demonstrates that dingoes and NGSD form a distinct cluster from domestic breed

dogs, village dogs and wolves (Figure 1). The first three principal components account for 44.13% (PC1), 19.83% (PC2) and 12.88% (PC3) of the variation in the data set. Phylogenetic reconstructions using Snphylo with 68 samples representative of different dingo, village dog, breed dog or wolf populations (Appendix) identifies that dingoes are closely related to south east Asian village dogs (Figure 2). There is a strong divergence between most extant dog populations (village dogs and breed dogs) compared to this Asian dog clade. There is strong (100%) bootstrap support for the dingo and NGSD branches. The split between the Asian and Eurasian clades is also strongly supported (100%).

Tremix phylogenetic reconstructions also observed a deep divergence between the Asian and Eurasian clades, with the dingo and NGSD sitting within this Asian clade (Figure 3). In our modelling the migration edge returning the highest get_f value was 10 migrations ($get_f = 95.9\%$). Modelling of migration between populations highlights the complex evolutionary history of dingoes, dogs and wolves (Figure 3). There is support for migration from the dingo/NGSD ancestor into some oceanic village dog populations, ancestors of the Malamute and into Asian dog lineages such as the Akita and Shiba Inu. There is little evidence of migration from the Eurasian dog clade into the dingo/NGSD lineage or the other Asian clade lineages. The Basenji is identified as having contributed to the identity of African village dogs, the Canaan dog and wolves. There is strong bootstrap support for the Asian clade branches (Figure 3). The Oceanic Tremix modelling shows that migration within Oceanic and Asian village dog populations is complicated (Figure 4). The best fit model, where $get_f = 99.8$, had 10 migration edges. There is evidence that the dingo/NGSD lineage contributed to the identity of village dogs in New Guinea and the Solomon Islands, and the Akita, Shiba Inu and Sharpei breeds. Migration modelling also identified a possible migration from the dingo/NGSD ancestor

into wolves. There was some evidence of domestic dog migration into southeastern Dingoes.

Discussion

Dingoes form a discrete evolutionary lineage, distinct and distinguishable from modern domestic dogs and wolves (Figure 1-4). East Asian dogs, dingoes and NGSD form an evolutionary lineage distinct from Eurasian domestic dogs including Central Asian, European, Middle Eastern, Indian, African and breed dogs (Figure 2-3). The Arctic dogs either form their own group outside of the Eurasian dog clade (Figure 2) or cluster with the Eurasian clade (Figure 3). The timing of the divergence between East Asian and Western dogs predates agriculture and hypothetically intensive domestication (Thalmann *et al.* 2013; Freedman *et al.* 2014; Fan *et al.* 2015; Pilot *et al.* 2015; Frantz *et al.* 2016; Freedman and Wayne 2017). Whilst dingoes fit within the East Asian dog phylogeny (Figure 2-3), they are genetically distinct from Asian village dogs and Asian domestic dog breeds (Figure 1). It is important to note that the evolutionary relationship between wolves, domestic dogs and dingoes has still not been fully untangled, whole genome data will hopefully provide further resolution. Fundamentally, it is not currently known where the original proto-dog arose and if they arose directly from modern wolves, from an extinct wolf, multiple times or as a natural species (Thalmann *et al.* 2013; Freedman *et al.* 2014; Fan *et al.* 2015; Pilot *et al.* 2015; Frantz *et al.* 2016; Freedman and Wayne 2017). Together these data would support dingoes being considered a discrete 'evolutionarily significant unit' to domestic dogs (Moritz 1994; Crandall *et al.* 2000).

Migration modelling within the East Asian dog lineage suggests that the dingo/NGSD lineage contributed to the ancestry of extant village dog populations in East Asia, Oceania and the Pacific (Figure 3-4). It is possible that the phenotypic resemblance between dingoes and East Asian

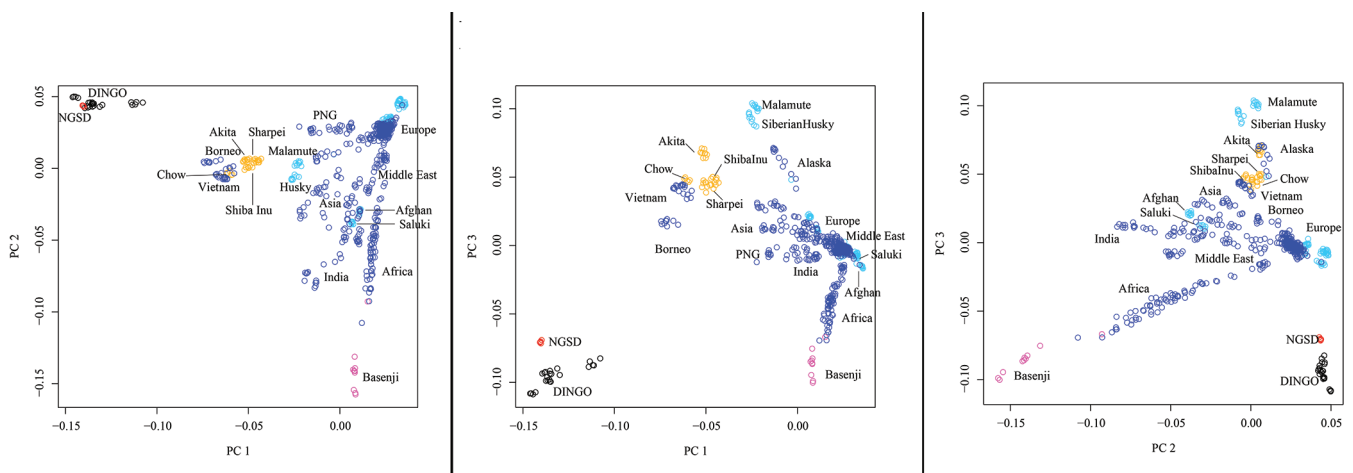


Figure 1. Principal Components Analysis (PCA) based upon filtered genome wide SNP genotypes (113,523 sites) from 657 samples across 65 canid populations or breeds. Colours represent population identity clusters: black for dingoes, red for NGSD, light green for wolves, orange for Asian breed dogs (Akita, Chow, Shiba Inu and Sharpei), dark blue for village dogs, aqua for modern domestic dog breeds and fuchsia for Basenji. (A) PC 1 versus PC 2. (B) PC 1 versus PC 3 and (C) PC 2 versus PC 3.

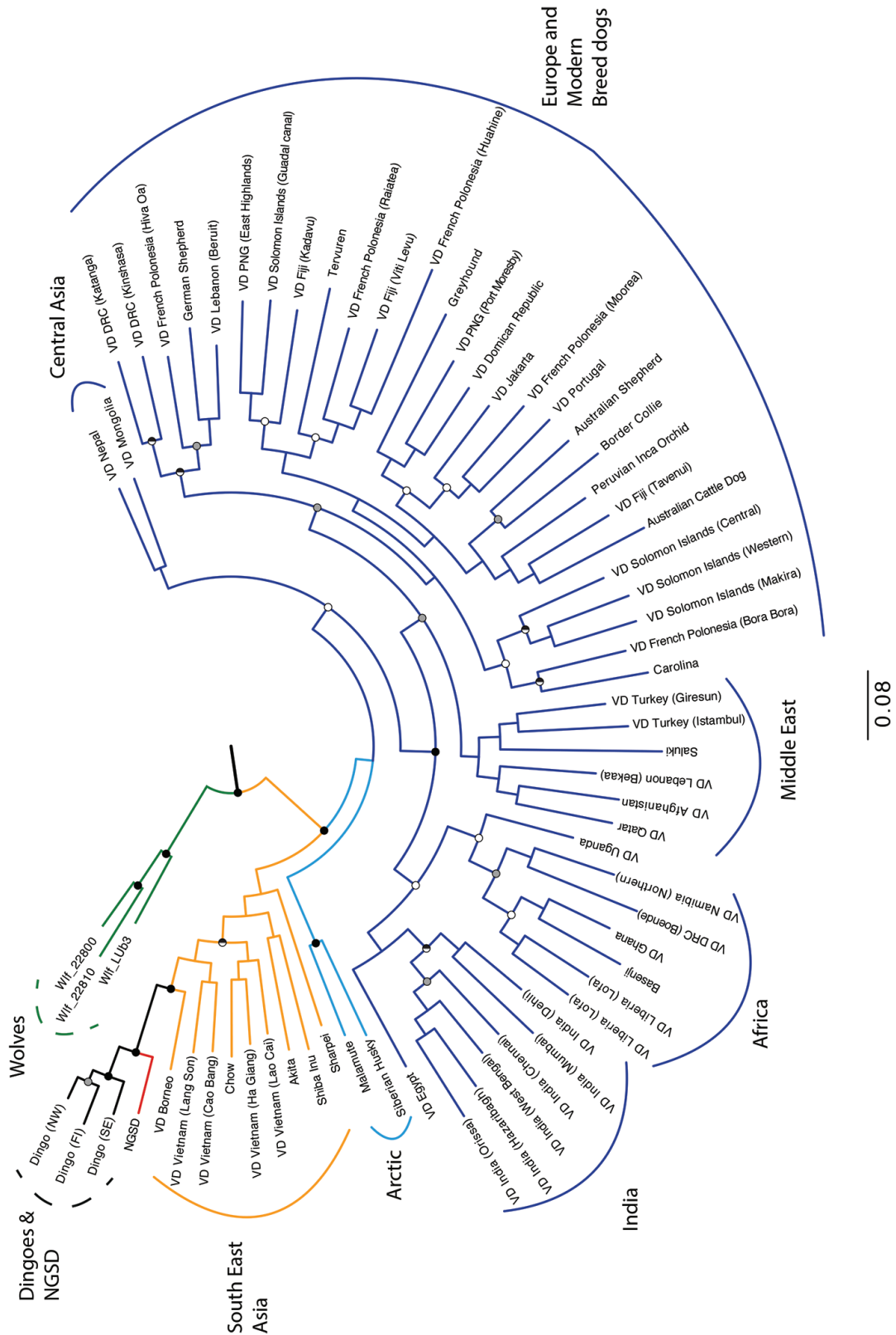


Figure 2. Maximum likelihood phylogeny constructed using SnpPhylo for wolves, dingoes, village dogs and breed dogs including 68 canid samples, bootstrapping was carried out using 200 replicates (Appendix). SnpPhylo trimmed the 143,156 SNP sites to 7,607 ancestry informative sites for building the maximum likelihood tree. Bootstrap support is shown by solid circles = 100% support, half solid circles = 96-99% support, solid grey circles = 90-95% support and open circles = 80-90% support. Village Dog populations are identified with the notation VD before the geographic region where the dogs were sampled from. The main clades are coloured as follows: East Asian is orange; Arctic is light blue; Eurasian is dark blue. Dingoes are shown in black and NGSD in red. Wolves are coloured dark green. Dotted lines indicate lineages that are wild living.

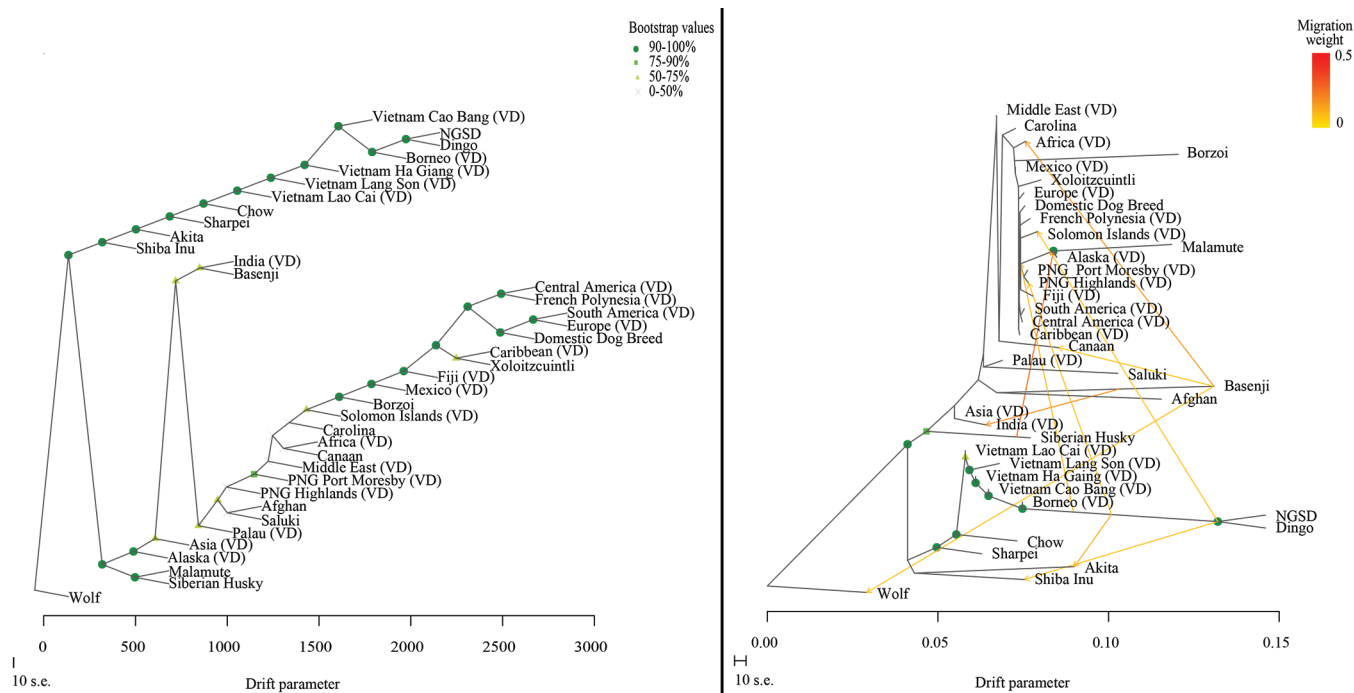


Figure 3. Phylogenetic analyses incorporating migration modelling for wolves, dingoes, village dogs and breed dogs. These reconstructions included 1022 samples across 39 populations or breeds (Appendix) and is based on 25,670 SNP sites. (A) Modelling with zero migration events. (B) Modelling with 10 migration events, explaining 95.9% of the variance in the data. Support for specific migration events (migration weight) is shown by the colour of the arrow, with darker red indicating higher support. Village Dog populations are identified with the notation (VD).

village dogs may be because the dingo/NGSD ancestral lineage admixed into East Asian village dogs (Figure 3-4), rather than because dingoes are the direct descendants of extant East Asian village dogs (Corbett 2001b; Corbett 2001a). This is consistent with Y-chromosome biogeography which observes that dingoes are an older evolutionary lineage that the village dogs found in Island South East Asia (Sacks *et al.* 2013). Migration modelling suggests that the dingo/NGSD ancestor may have contributed to the identity of some Oceanic village dog populations as well (Figure 4). These hypothesised admixture events warrant further interrogation with additional genomic and bioinformatic analyses. Regardless, the long branch lengths leading to the NGSD/Dingo lineage suggest that these populations have been reproductively isolated from extant domestic dogs for a lengthy period of time (Figure 2-4). The hypothesised added complexity of canid migration across time and space is an important consideration in our understanding of the evolutionary history of dogs, dingoes and wolves. Future studies should incorporate advanced migration modelling between dog lineages, dingoes and different wolf populations to verify possible migration events and further untangle the history of canids across the world.

Genome-wide SNP data demonstrate that dingoes and NGSDs are close relatives (Figure 1-4). This is consistent with hypotheses that dingoes immigrated to Australia through the island of New Guinea via a land bridge (Cairns and Wilton 2016; Cairns *et al.* 2017; Cairns *et al.* 2018). This finding is also consistent with the similarity in cranial morphology observed between dingoes and NGSDs (Koungoulos 2020). A majority of the NGSD

population is kept in captivity in North America, founded by 8 individuals captured from the wild in 1950 (Koler-Matznick *et al.* 2004). It was once believed that NGSDs were absent or very low density in the wild, however, discovery of New Guinea Highland Wild Dogs living in the highlands of New Guinea at 3900 – 4170 m elevation suggest that this unique population is persisting (McIntyre *et al.* 2019). The occurrence of these dog lineages in remote and harsh environments as free-living and wild populations is suggestive that these taxa are remnant populations of the proto-dog, close relatives of the dingo, rather than feral village dogs (McIntyre *et al.* 2019). There are still knowledge gaps concerning where, when and how the dingo arrived in Australia, although molecular dating suggests dingoes may have immigrated to Australia 6,000-8,000 years BP via a land bridge (Cairns and Wilton 2016; Cairns *et al.* 2017; Cairns *et al.* 2018). Arguably the length of time that the dingo and NGSD have been isolated, along with evidence of morphological and genetic divergence would support dingoes and NGSD being treated as separate evolutionarily significant units. Continued investigation of the relationships between dingoes, the New Guinea Highland Wild Dogs and NGSDs will be important in resolving the origins of these proto-dogs, nomenclature and their conservation status.

Eurasian domestic dogs form the majority of pet and free living dog populations around the world – including village dogs from India, Africa, Middle East, South America, mainland Asia; historical dog breeds such as the Basenji, Afghan Hound, Saluki; and modern domestic dog breeds such as the Pug, Labrador, Beagle (Figure 2-3). Contrary

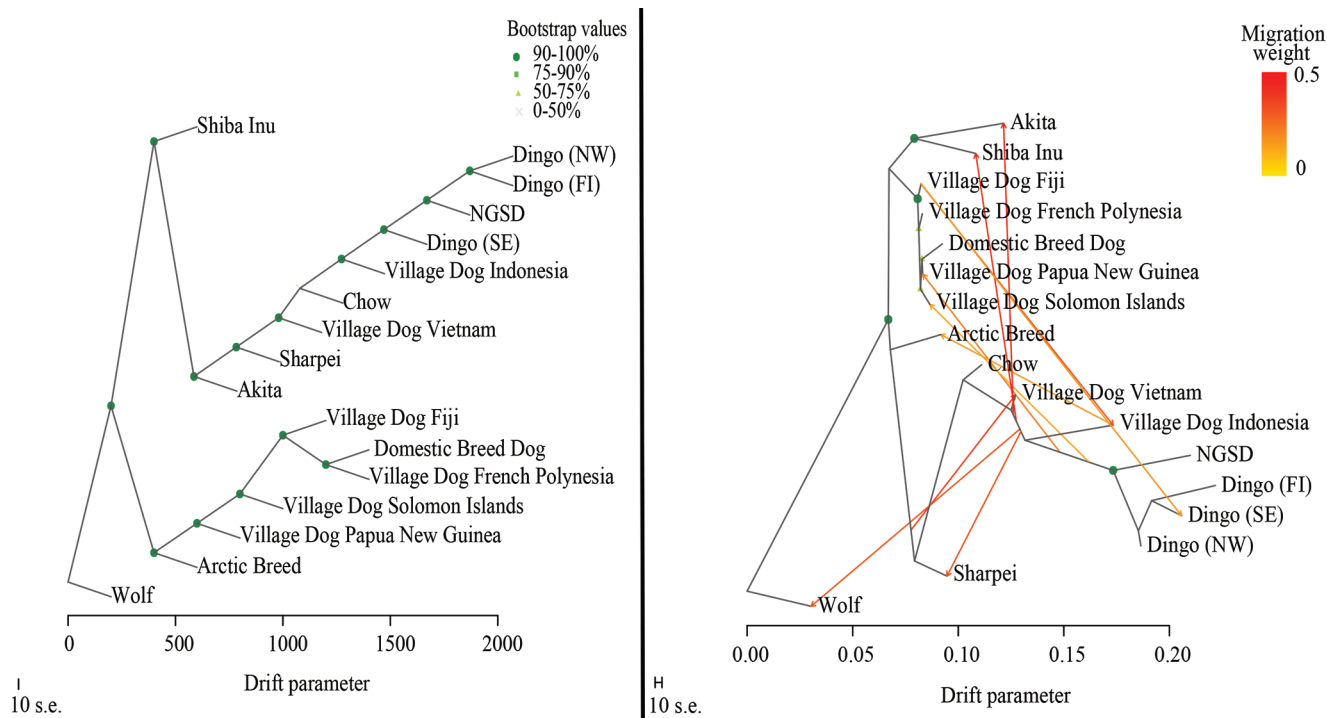


Figure 4. Phylogenetic analyses incorporating migration modelling for Oceanic dogs and dingoes. These analyses included 246 samples across 25 populations or breeds (Appendix) and is based on 56,156 SNP sites. (A) Modelling with zero migration events. (B) Modelling with 10 migration events, explaining 99.8% of the variance in the data. Support for specific migration events (migration weight) is shown by the colour of the arrow, with darker red indicating higher support.

to the findings of vonHoldt *et al.* (2010), the Basenji is not basal to dingoes, Arctic dogs and Asian dogs (Figure 1-3). It is important to point out that the phylogeny presented by vonHoldt *et al.* (2010) fails to recognise the evolutionary distinction between Asian and Eurasian dogs because their dataset contains predominately modern domestic breed dogs. Future genomic research should take care to include representatives of dingoes, NGSD, Asian village dogs, Eurasian village dogs and modern domestic dog breeds to avoid geographic bias or a lack of resolution between Asian and Eurasian dog lineages. Instead we observe that dingoes share an evolutionary lineage with East Asian dogs (Figure 2-3). Although, there are some Asian domestic dog breeds such as the Sharpei, Chow Chow and Akita that fall within the East Asian dog lineage, these may have evolved through admixture with Eurasian domestic dogs or artificial selection by humans. Indeed, migration modelling suggests that breeds such as the Sharpei, Akita and Shiba Inu may be European lineages with admixture from the dingo/NGSD ancestor (Figure 4). It is possible that historical admixture between lineages is biasing phylogenetic reconstructions, warranting further research aimed at resolving the admixture history of Asian breed, Asian village dog and wild canid (dingo and NGSD) lineages.

The continuum of domestication, species names and conservation

Jackson *et al.* (2017; 2019) consider that all dogs are domesticated, and thus their nomenclature should be *Canis familiaris*. They consider that dogs evolved directly,

through domestication, from the holoarctic wolf (*Canis lupus*). However, genomic studies of the evolutionary history of dogs, dingoes and wolves have observed that modern wolves may not be the direct ancestor of the dog/dingo but rather a now extinct Pleistocene wolf (Thalmann *et al.* 2013; Freedman *et al.* 2014; Fan *et al.* 2015; Freedman and Wayne 2017). This implies that whilst modern wolves are the closest relative to the dingo and domestic dog, they may not be the direct ancestor. Crowther *et al.* (2014) suggest that dingoes form a diagnosable taxon divergent from domestic dogs and because their exact evolutionary origins are unknown, they were reproductively isolated and they are wild living, the most appropriate nomenclature for them is *Canis dingo*. Smith *et al.* (2019) consider that dingoes are an early wild form of the dog, which has not undergone domestication or “complete” domestication. Extensive DNA testing across Australia demonstrates that survivorship of feral domestic dogs in the wild is poor (Stephens *et al.* 2015; Cairns *et al.* 2019). This suggests that dingoes are not interchangeable with domestic dogs and therefore should be recognised in terms of nomenclature and taxonomy as distinct from domestic dogs, who are a man-made domestic species.

The data presented here demonstrates that the evolutionary history of history of dogs, dingoes and domestic dogs is much more complex and multi-faceted than presented by Jackson *et al.* (2017; 2019). There are multiple lineages of dog and the split between East Asian and Eurasian dogs is deep, possibly predating agriculture and intensive domestication (Brown *et al.* 2011; Axelsson *et al.* 2013; Brown *et al.* 2013; Freedman *et al.* 2014; Brown

et al. 2015; Pilot *et al.* 2015; Arendt *et al.* 2016; Frantz *et al.* 2016; Freedman and Wayne 2017). Dingoes are a basal lineage of the East Asian dog, one that exists in a wild state and has done so for thousands of years. Whilst dingoes have been largely isolated from other canid lineages, many village dog populations in Asia now share ancestry with European dogs. Zhang *et al.* (2020) present evidence that dingoes have undergone genomic adaptation since arriving in Australia approximately 8,000 years ago. Together these data support dingoes and NGSD being treated as discrete evolutionarily significant units.

Dingoes feature heavily in the spiritual and cultural identity of First Nations Australians. Indeed in some cases First Nations people kept pups (generally sourced from the wild) and raised them as tame companions, guardians, 'bed warmers' and hunting (Smith and Litchfield 2009; Koungoulos and Fillios 2020). However, there is little morphological, behavioural, ecological, biological or genetic evidence to suggest that dingoes were a domesticate (Ballard and Wilson 2019; Smith *et al.* 2019; Koungoulos and Fillios 2020). As a population dingoes are morphologically, behaviourally and genetically distinguishable from domestic dogs, particularly Eurasian ones, despite the close phylogenetic relationship between dingoes and domestic dogs. The dingoes' distinct evolutionary lineage is representative of a shared ancestry with dogs, followed by geographic isolation and adaptation to the Australian environment.

In a practical sense, based on both ICZN Opinion 2027 and Gentry *et al.* (2004), domesticates and wild forms may retain different species names, particularly if the "...wild species and their derivatives are recognisable entities". I suggest that since dingoes and domestic dogs may be distinguished based on a variety of genetic, morphological, biological, evolutionary and ecological lines of evidence (Crowther *et al.* 2014; Smith *et al.* 2019) it would be appropriate to use *Canis familiaris* for domestic dog populations and *Canis dingo* for remnant wild pre- or peri-domesticate populations such as dingoes and NGSD. In this way, nomenclature can appropriately and practically assist wildlife workers to consider the different management, conservation and evolutionary identities of dingoes or NGSD versus domestic dogs.

Jackson *et al.* (2017; 2019) suggested that to elevate dingoes to species level would require elevating all domestic dog breeds to species level. This does not follow logically, domestic dog breeds are not wild living proto-dogs and most extant village dog and dog breeds are from the Eurasian dog lineage which has been heavily influenced by domestication (Figure 2-3). A majority of domestic dog breeds arose only in the last 250 years and are entirely human constructs formed through artificial selection (vonHoldt *et al.* 2010; Axelsson *et al.* 2013; Freedman *et al.* 2016; Parker *et al.* 2017; Pendleton *et al.* 2018). Indeed, according to principal components analyses of genome-wide SNP data dingoes and NGSD,

the wild proto-dogs are clearly distinct from both Asian and Eurasian domestic dogs (Figure 1). The only logically consistent implication might be to consider some East Asian dogs, of the same ancestral phylogenetic lineage to dingoes, to be *Canis dingo*, but application of the opinions expressed by ICZN Opinion 2027 and in Gentry *et al.* (2004) would suggest that this only be applied to truly wild living dog populations such as dingoes, the New Guinea Highland Wild Dog and NGSD. Furthermore, it would be defensible for this nomenclature to only apply to East Asian dog lineages that have not undergone considerable historical admixture with European dogs (Figure 3-4), excluding most extant village dog populations.

Moving forwards, conversations about dingo nomenclature must rely upon multiple lines of evidence to assess the case for species status, including phylogenetics, diagnosable genetic identity, morphology, behaviour, ecology and biology (Smith *et al.* 2019). Strong consideration must be given to the complex evolutionary history of canids and assumptions about domestication status should be critically evaluated. When considering canids there is support for unique evolutionary lineages, like the dingo, Himalayan wolf or red wolf to be considered separate species from wolves, coyotes and domestic dogs, while acknowledging that they all occupy the same species complex more broadly (Gopalakrishnan *et al.* 2018; Murphy *et al.* 2018; vonHoldt *et al.* 2018; National Academies of Sciences and Medicine 2019; vonHoldt and Aardema 2020; Werhahn *et al.* 2020). Regardless, scientists continue to agree that dingoes form an ecologically and evolutionarily significant unit with high conservation value (Jackson *et al.* 2017; Cairns *et al.* 2018; Ballard and Wilson 2019; Jackson *et al.* 2019; Smith *et al.* 2019; Zhang *et al.* 2020), and this needs to be properly reflected in Australian conservation management programs.

Population subdivision and implications for hybridisation estimates

Studies focusing on maternal (Cairns and Wilton 2016), paternal (Cairns *et al.* 2017) and genome-wide markers (Cairns *et al.* 2018), as well as cranial morphology (Koungoulos 2020) have identified the presence of multiple evolutionary lineages of dingo that are geographically subdivided (Figure 5). Southeastern dingoes appear to share a closer maternal relationship with the NGSD and are restricted to the southern and eastern coastal regions of Australia (Cairns and Wilton 2016; Cairns *et al.* 2017). The northwestern dingo population is widespread across western, northern and central Australia and shares a close paternal relationship with the NGSDs (Cairns *et al.* 2017).

For decades, there has been concern about domestic dog hybridisation with dingoes, some scientists have hypothesised that dingoes will be replaced by feral domestic dogs or dingo-dog hybrids (Newsome and Corbett 1985; Corbett 2001a; Corbett 2001b; Fleming *et*

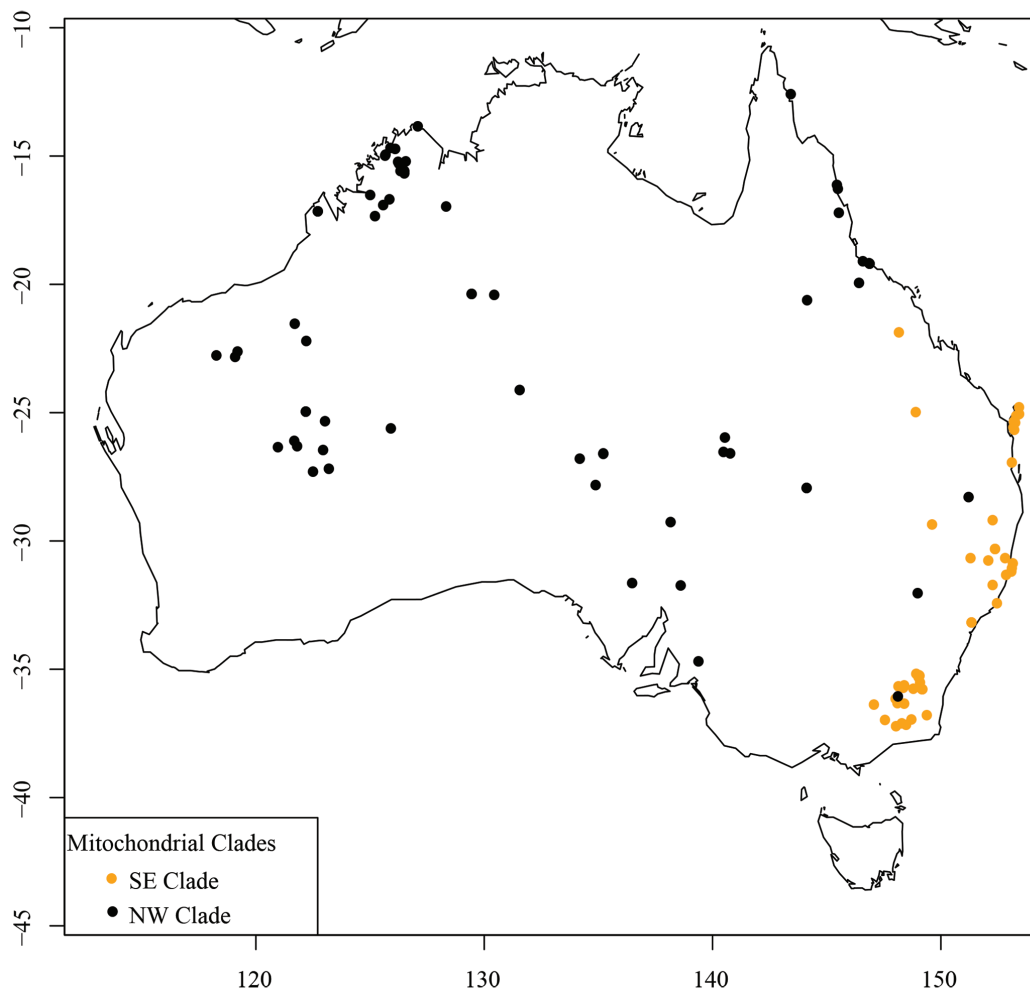


Figure 5. A map depicting genetic subdivision of dingoes across Australia based on mitochondrial DNA (mtDNA) with black circles indicating dingoes harbouring a northwestern mtDNA haplotype and orange circles representing dingoes with a southeastern mtDNA haplotype. Reprinted under the Creative Commons Attribution License from “Conservation implications for dingoes from the maternal and paternal genome: Multiple populations, dog introgression, and demography,” by K.M. Cairns S.K. Brown, B.N. Sacks and J.W.O. Ballard, 2017, *Ecology and Evolution*, 7 (22), 9787-9807.

al. 2001; Daniels and Corbett 2003; Elledge *et al.* 2006; Glen 2010; Claridge *et al.* 2014; Stephens *et al.* 2015). This concern has led to widespread use of the term “wild dog” as an umbrella for all Australian wild living canids. Initially skull morphology was used to distinguish between “pure” and “hybrid” dingoes, by comparing an unknown skull to a reference set of dog or dingo skulls (Newsome *et al.* 1980; Newsome and Corbett 1982). However, Parr *et al.* (2016) found that skull morphology is highly conserved in dingoes and dingo hybrids, calling into question the reliability of ancestry assessments based entirely on skull morphology.

In the 1990s a microsatellite DNA test was developed for estimating the extent of dingo vs dog ancestry in an animal (Wilton *et al.* 1999; Wilton 2001; Elledge *et al.* 2008). Similar to with skull morphology methods, the DNA testing methodology relies upon comparing unknown samples to defined reference populations of “pure” dingoes and domestic dogs (Wilton 2001; Elledge *et al.* 2008; Stephens *et al.* 2015; Cairns *et al.* 2019). Stephens *et al.* (2015) undertook DNA testing

of 4,500 animals across Australia to examine the extent of domestic dog admixture in dingoes. They found that southeastern Australia had high levels of domestic dog introgression with an estimated 99% of the population estimated to carry some domestic dog genes (Figure 5). They estimated that of the NSW population only 1% were pure dingoes and 21% were probable pure dingoes, based on 95 samples. Cairns *et al.* (2019) report a higher incidence of 2% pure and 21% likely pure dingoes in north-eastern NSW based on a survey of 783 animals, but also observed that a high proportion of the dingo population carries some dog genes. These findings highlight the need to better balance our conservation and management of dingoes, particularly in southeastern Australia. This data also indicates that the term “wild dog” is not accurate or appropriate because across Australia, the wild canid population carries predominately dingo ancestry. Feral domestic dogs and low ancestry dog hybrids (less than 50% dingo ancestry) are rare occurrences in the wild. Modifications in management should be aimed at preventing future hybridisation events and minimising the spread of further

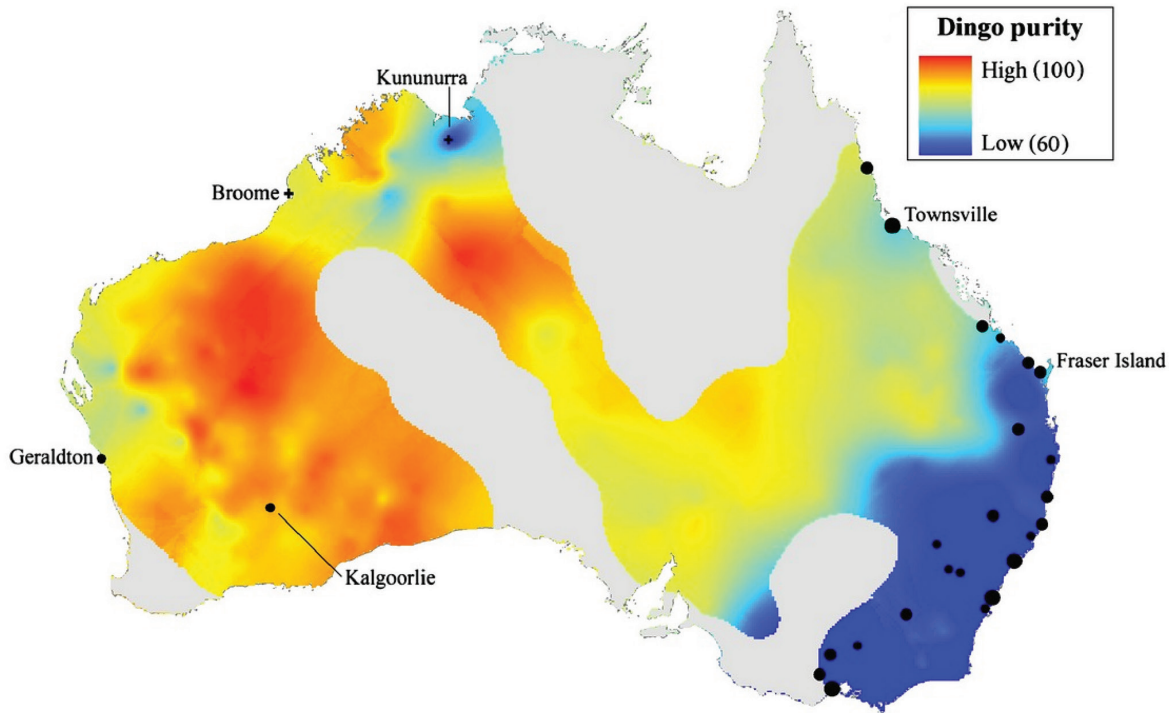


Figure 6. A kriging map of dingo DNA ancestry across Australia from Bayesian DNA clustering ancestry estimates based on 23 microsatellites. Reprinted with permission from “Death by sex in an Australian icon: a continent-wide survey reveals extensive hybridization between dingoes and domestic dogs,” by D. Stephens, A.N. Wilton, P.J.S. Fleming and O. Berry, 2015, *Molecular Ecology*, 24 (22), 5643-5656.

dog genes into the dingo population. Conservation efforts should focus on preserving dingo populations with high dingo ancestry, particularly those in conservation areas such as National Parks. Management plans need to consider the occurrence of divergent evolutionarily significant lineages (Cairns *et al.* 2018). Ongoing genetic monitoring of dingo populations across Australia, particularly where lethal control is used, should continue to identify conservation hotspots versus regions where lethal control is favouring hybridisation.

There are very similar distributions of evolutionary geographic subdivision (Figure 5) and higher incidence of domestic dog ancestry in dingoes from south-eastern Australia, this bears interrogation. It is possible that geographic subdivision in dingoes may be biasing hybridisation methods and steps need to be taken to control for geographic bias (Cairns and Wilton 2016; Cairns *et al.* 2017; Cairns *et al.* 2018; Cairns *et al.* 2019; Koungoulos 2020). Both skull morphology (Newsome *et al.* 1980; Newsome and Corbett 1982; Newsome and Corbett 1985; Jones 1990; Woodall *et al.* 1996; Corbett 2001b; Elledge *et al.* 2008; Jones 2009) and current DNA testing methods (Wilton 2001; Elledge *et al.* 2008; Stephens *et al.* 2015; Cairns *et al.* 2019) rely upon geographically restricted and pre-defined reference populations of “pure” dingoes. It is possible that if dingoes in one region are genetically or morphologically divergent, then current hybridisation estimation methods may identify those animals as hybrids, rather than ‘different’ dingoes. First, I suggest that users of

dingo ancestry DNA testing assess whether the reference population used is representative of the dingoes in their study region. Second, DNA testing users should critically assess results if high numbers of rare alleles are observed in a specific dingo population or animal. High proportions of rare alleles indicate that those alleles have not been observed in either the reference domestic dog or reference dingo populations, suggesting the presence of geographic variation in the animal or dingo population or influence from an unusual domestic dog breed. I suggest that future genetic monitoring and research should seek to employ high-density genomic data which provides better utility and accuracy in assessing domestic dog introgression (Cairns *et al.* 2011), preferably removing the need for geographically biased reference populations (Cairns *et al.* 2019). Ongoing research into the identity of dingoes across Australia, may assist in progressing debate about the conservation status of dingoes and help build appropriate management plans that balance conserving dingoes in the natural landscape with the need to reduce livestock predation.

Final conclusions

Despite persisting knowledge gaps about the exact relationship between wolves, dingoes and domestic dogs, dingoes represent an important and distinct population of truly wild canid. The wild lifestyle of dingoes is a fundamental functional difference between domestic dogs and dingoes, strongly demonstrating that they are not interchangeable taxon.

Genomic comparisons to dogs and wolves from across the world demonstrate that dingoes share a close phylogenetic relationship with but are a distinct entity from domestic dogs. Dingoes are a wild remnant population of the Asian dog lineage and as such the most appropriate nomenclature should be *Canis dingo*, distinct from the domestic dog *Canis familiaris*, a man-made domesticate. Future research investigating the evolutionary history and domestication status of dingoes should include NGSDs, Highland Wild Dogs and Asian village dogs rather than relying upon comparison to modern domestic dog breeds.

When considering taxonomy in canids, I err with Crowther *et al.* (2014) and Smith *et al.* (2019), suggesting that arguments for taxonomic distinction must rely upon multiple lines of evidence including phylogenetics, diagnosable genetic identity, morphology, behaviour, ecology and biology. It is demonstrable that dingoes have not undergone the same evolutionary processes as domestic dogs, form a distinguishable population and that they are a wild living 'evolutionarily significant unit'. Furthermore, it is defensible and practical for wild canid

lineages, like the dingo or red wolf to be considered separate species from wolves, coyotes and domestic dogs, while acknowledging that they all occupy the same species complex more broadly. The evolutionary distinctiveness and ecological importance of dingoes to Australia needs to be properly reflected in environmental management and conservation legislation.

The presence of population subdivision in dingoes raises questions about the accuracy of existing DNA and skull morphology methods to detect dog introgression into dingo populations. There are several evolutionarily significant lineages of dingo (Cairns *et al.* 2018) and management action plans need to target protection for at risk populations. Reliance on geographically restricted pre-defined dingo reference populations has the potential to bias hybridisation estimates, users of current DNA testing methods are cautioned to critically assess hybridisation estimates. I suggest that future genetic monitoring and research on the genetic identity of dingoes' use genome-wide SNP technologies to assess domestic dog introgression.

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Methods and Materials

Genetic data

I use Illumina CanineHD 170K genotype data collected by Vaysse *et al.* (2011), Shannon *et al.* (2015) and Cairns *et al.* (2018) to explore the evolutionary history of dingoes compared to free-breeding village dogs, breed dogs and some wolves from across the world. Specifically, the dingo Canine HD 170K genotype data was collected from 24 dingoes that were estimated by microsatellite DNA testing to be free from domestic dog introgression and representing five geographic regions across Australia: the Kimberley, the Gibson Desert, the Simpson Desert, K'Gari (Fraser Island) and the Australian Alpine Region (Cairns *et al.* 2018). The dog data collected by Vaysse *et al.* (2011) and Shannon *et al.* (2015) includes representatives of many modern domestic dog breeds, as well as village dogs from across the world. A total of 14 wolf samples were included in the study representing North American, Middle Eastern and Israeli populations (Vaysse *et al.* 2011). Briefly, genotype data was downloaded, formatted and merged using Plink v1.9 (Purcell *et al.* 2007). Filtering was completed to remove individuals with low genotyping rate using `--geno 0.1`. To remove regions with high linkage disequilibrium, pruning was undertaken using the command `--indep-pairwise 20 5 0.6` in Plink v1.9. Prior to phylogenetic and migration modelling, Vcftools (Danecek *et al.* 2011) was used to remove sites with missing data and Stacks v2.41 (Catchen *et al.* 2013) was used to format the data. The samples used for each analysis are reported in online Table S1.

Principal components analysis

Principal components (PC) analysis was run in Plink v1.9 on the filtered and linkage pruned dingo, dog and wolf dataset, using the `--pca` function. Plots were made comparing PC1 to PC2, PC2 to PC3 and PC1 to PC3, this was done in R (R Development Core Team 2010).

Phylogenetic reconstruction

The phylogenetic relationships between dingoes, regional village dogs, breed dogs and wolves were reconstructed using two different methods: SNPhylo (Lee *et al.* 2014) and Treemix (Pickrell and Pritchard 2012). For the SNPhylo analysis, only a single individual dog, dingo or wolf was used from each population. SNPhylo is a pipeline that creates a maximum likelihood tree from large SNP datasets by several steps: (1) removing low quality data, (2) filtering for representative SNPs, (3) creating a sequence alignment for each individual, (4) using DNml (Felsenstein 1989) to create a phylogenetic tree and (5) bootstrapping of the phylogenetic tree. SNPhylo was run with linkage pruning (`-l 0.1`) and 500 bootstrap replicates (`-b -B 500`).

Treemix was also used to reconstruct phylogenetic relationships between dingoes, village dog, domestic dog breed and wolf populations using the SNP data. For this analysis, canids from the same population or breed were pooled for analysis, such that the input file represents the observed allele frequencies for each SNP in each species, locality or breed population. Initial Treemix reconstructions were based on 1022 samples across 39 populations or breeds, after filtering to remove sites with missing data a total of 25,670 SNP sites remained. For these analyses 449 modern breed dog samples from were pooled together as “Domestic Breed Dogs”. Bootstrapping was carried out in Treemix using BITE (Milanesi *et al.* 2017). Treemix bootstrap analyses were carried out using increasing migration edges to investigate the likelihood of admixture between dingo, wolf and dog populations. Migration edges were increased from 1 to 10, with the `get_f` function indicating the amount of variance that the model accounts for (Pickrell and Pritchard 2012). The model with the highest `get_f` value was chosen as the best fit for the data.

Additional analyses were carried out in Treemix using a reduced sample set of oceanic and Asian village dogs, some modern dog breeds, New Guinea Singing Dogs, dingoes and wolves to model migration between Asian and Oceanic dogs and dingoes. Specifically, the Oceanic Treemix reconstructions included 246 samples across 25 populations or breeds, and after filtering to remove sites with missing data a total of 56,156 SNP sites remained. The 20 Malamute and Siberian Husky samples were pooled together as ‘Arctic Breed’ and 49 modern breed dogs were pooled together as ‘Modern Breed’, these served as a comparison to identify European or Arctic breed admixture into Asian village dog, Oceanic village dog, NGSD or dingo populations (Table S1). Again, bootstrap analyses were carried out with Treemix and BITE, adding migration edges from 1 to 10. The model with the `get_f` value closest to 99.8 was chosen as the best fit for the data (Pickrell and Pritchard 2012).