

Introgression does not influence the positive ecological and functional role of dingo populations

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ABSTRACT

The impact of hybridisation between dingoes and domestic dogs, and the subsequent introgression of domestic dog genes into dingo populations, remains a topic of significant impact. It has been claimed, but with little evidence or logical argumentation, that dingoes with significant dog introgression have different effects on agriculture and ecosystems than dingoes with no dog introgression. Introgression is a natural process in evolution, occurring in many species, although this is sometimes human assisted. Canid species in particular show high levels of introgression, due to their genetic and phylogenetic similarities, and human persecution creates scenarios encouraging hybridisation. Dingoes are no exception and demonstrate high levels of introgression of domestic dog genes, particularly in the temperate areas of south-eastern Australia. The available evidence shows that this introgression has minimal effects on the functional morphology of the dingo skull. There is also some preliminary evidence that introgression has not had a major impact on dingo reproductive biology. Studies on the impacts of dingoes on arid, tropical and temperate ecosystems, where levels of introgression vary greatly, all show consistent positive impacts of dingoes, regardless of the amount of domestic dog genes within the dingo population, on these ecosystems. Hence, hybridisation and resultant introgression from domestic dog genes appear to have little effect on aspects of the functional morphology or ecological role of the dingo. Accordingly, introgression does not diminish the conservation status of the dingo.

Key words: dingo; hybridisation; introgression; canids; trophic cascades; phenotype; functional morphology; mesopredator release; geometric morphometrics

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Introduction

The topic of hybridisation of the dingo (*Canis dingo*) with the domestic dog (*C. familiaris*), and the introgression of dog genes into dingo populations, is the source of many debates, from taxonomic, ecological, agricultural and cultural standpoints (Crowther *et al.* 2014, Smith *et al.* 2019, van Eeden *et al.* 2019). Frequently these arguments question the dingo's taxonomic distinctiveness due to past introgression, and suggest that dingo-dog hybrids have negative impacts on ecosystems and on livestock. However, much of the debate on how much introgression has occurred in dingoes or how much this affects their ecological role and agricultural impacts is based on very little data and no scientific argumentation. Here, we examine what is introgression, how much introgression of dog genes there may be in the dingo population, and what likely effects this has on the phenotype and ecological role of the dingo.

What is introgression?

Hybridisation is the interbreeding of individuals from genetically distinct populations, regardless of the taxonomic status of those populations (Rhymer and Simberloff 1996). Most commonly it refers to mating between different species but has been applied to different subspecies and populations. Introgression is the gene flow between the populations whose individuals hybridise, and is achieved when hybrids repeatedly backcross to one or both parental populations (Rhymer and Simberloff 1996).

Hybridisation and introgression are very common phenomena, with up to 25% of plant species and 10% of animal species involved in hybridisation and potential introgression (Mallet 2005). These percentages are based on "natural" occurrences of hybridisation in that they exclude all introduced species hybridisation, even though some may be the indirect result of habitat degradation (Mallet 2005). Examples of hybridisation

include introgression in many species of *Eucalyptus* tree (Field *et al.* 2011), hybridisation between salmonid fish species (Blanc and Chevassus 1979, Chevassus 1979, Muhlfeld *et al.* 2014), introgression of cattle genes into American bison (*Bison bison*) (Halbert and Derr 2007), introgression of brown (*Ursus arctos*) and polar bear (*U. maritimus*) genes (Miller *et al.* 2012, Pongracz *et al.* 2017) and between the domestic cat (*Felis catus*) and European/Scottish wildcat (*Felis silvestris*) (Beaumont *et al.* 2001, Hertwig *et al.* 2009, Macdonald *et al.* 2010, Tiesmeyer *et al.* 2020).

Introgression has also shaped the genome of humans (*Homo sapiens*), with extensive introgression of Neanderthal (*H. neanderthalensis*) and Denisovan genes into the *H. sapiens* gene pool (Sankararaman *et al.* 2014, Sankararaman *et al.* 2016). Hence, the strict application of the biological species concept (*sensu* Mayr 1970), in which different species should not produce fertile young, is not applicable to many species. Introgression also may have some adaptive advantages such as the increase in range of brown bears with polar bear gene introgression (Cahill *et al.* 2015) or wolves having increased resistance from canine distemper due to dog introgression (Hendricks *et al.* 2019). However, other species are threatened by introgression (Rhymer and Simberloff 1996) and introduced species are threatening the extinction of local plant species (Levin *et al.* 1996, Vilà *et al.* 2000), while climate change is causing increased hybridisation and threats of extinction in fish (Muhlfeld *et al.* 2014).

Introgression in canids

Introgression is particularly common in canid species, of the genus *Canis* (Gopalakrishnan *et al.* 2018). This is because all are phylogenetically very close (vonHoldt *et al.* 2013), and all share the same number of chromosomes (78) (Wayne and Ostrander 1999). The red wolf (*Canis rufus*) of the southern United States of America, is considered to be a distinct taxon that may be the result of historical coyote (*Canis latrans*) gene introgression into grey wolves (*Canis lupus*) (National Academies of Sciences Engineering Medicine 2019, Nowak 1992, Wayne and Jenks 1991). Hybridisation and introgression between coyotes and wolves has been observed in regions where the two species overlap in North America (Bohling *et al.* 2017, Kays *et al.* 2010, vonHoldt *et al.* 2016, vonHoldt *et al.* 2011). Scientists have also observed coyote-dog hybrids, golden jackal (*Canis aureus*)-dog hybrids (Galov *et al.* 2015), and wolf-dog hybrids (Donfrancesco *et al.* 2019, Hindrikson *et al.* 2012, Vilà and Wayne 1999, vonHoldt *et al.* 2013). Historical adaptive introgression from domestic dogs into grey wolves in Northern America approximately 1,500-7,200 years ago is responsible for the spread of black coat colour in wolves (Schweizer *et al.* 2018).

Hybridisation between canid species may be higher in areas of canid persecution by humans (Hendricks *et al.*

2019). In circumstances where a canid population is persecuted through lethal control, this may lead to low population densities and fracturing of pack structures, which may increase the risk or enable hybridisation (Hendricks *et al.* 2019, Koblmüller *et al.* 2009, Lehman *et al.* 1991, Roy *et al.* 1994, vonHoldt *et al.* 2016, vonHoldt *et al.* 2011, Wayne and Jenks 1991). This has led to debate about how to manage or conserve canid species or populations that might be admixed or carry introgressed domestic dog genes (Donfrancesco *et al.* 2019, Hendricks *et al.* 2019, van Eeden *et al.* 2019, vonHoldt *et al.* 2017).

Introgression and the dingo (*Canis dingo*)

Since European settlement, there has been introgression of domestic dog genes into the dingo population. Genetic degradation as a result of introgression has been considered justification for listing dingoes as threatened under the *Victorian Flora and Fauna Guarantee Act 1988* and the IUCN Red List. Wilton *et al.* (1999) and Wilton (2001) developed a DNA test for estimating levels of domestic dog introgression within dingoes based on 21 microsatellites and 2 indel markers, often referred to as the “average 3Q” test. Stephens *et al.* (2015), using the average 3Q and Bayesian clustering methods, recorded relatively low introgression in central and northern Australia, with 87% considered “pure dingoes” (free from domestic dog introgression) in the Northern Territory based on 24 microsatellites. In contrast, in south-eastern Australia they estimated that 99% of dingoes had some domestic dog ancestry (Stephens *et al.* 2015). However, application of this test widely across Australia has been questioned because it uses arbitrary thresholds for dingo “purity” (Cairns *et al.* 2020). Furthermore, it is possible that the current microsatellite methods may inflate estimation of domestic dog introgression because of geographic variation within dingoes. Indeed, this DNA test was developed before it was known that there are multiple lineages of dingo across Australia, as revealed through sequencing of mitochondrial, Y-chromosome and nuclear DNA (Cairns *et al.* 2017, Cairns *et al.* 2018, Cairns and Wilton 2016). Stephens *et al.* (2015) also used a smoothing method (kriging) to map ancestry across Australia and because of limited sampling in NSW did not observe the newly identified hotspots of high dingo genetic ancestry in New South Wales (Cairns *et al.* 2020, van Eeden *et al.* 2019). An important finding of both Stephens *et al.* (2015) and Cairns *et al.* (2020) is the very low incidence of feral domestic dogs with no dingo ancestry, suggesting that domestic dogs do not survive well in the wild (Smith *et al.* 2019). Nevertheless, introgression of dog genes appears to be higher in the areas with longer European settlement and where contemporary human population densities are greater, such as south-eastern Australia (Cairns *et al.* 2020, Stephens *et al.* 2015).

Phenotypic effects of introgression in the dingo

Assessing the phenotypic effects of introgression in dingoes is difficult due to the extremely high morphological variation within the domestic dog (Drake and Klingenberg 2010). Although there are some colour variations in dingoes attributed to introgression (Cairns *et al.* 2011, Crowther *et al.* 2014, Smith *et al.* 2019), unlike in wolves, where black wolves have higher annual survival, lifespan, and lifetime reproductive success, there is currently no evidence for these colour variations having any adaptive value (Schweizer *et al.* 2018), however this may be research for the future. Earlier attempts to morphologically separate dingoes from domestic dogs have also suffered from the unknown ancestry of wild dingoes (Newsome and Corbett 1982, Newsome *et al.* 1980). However, by restricting dingo samples to pre-European contact, or when European contact was sparse (<1900 CE regional Australia), there are some diagnosable morphological characteristics separating dingoes from domestic dogs (Crowther *et al.* 2014). These characteristics include larger palatal widths, longer rostra, shorter skull heights, and wider temporal ridges of the skull (Crowther *et al.* 2014, Smith *et al.* 2019). Importantly, due to the great range of pelage colourations possible in dingoes (Crowther *et al.* 2014), it is not possible to use pelage colouration to diagnose dingoes from dingo-dog hybrids.

One way of examining whether introgression has any functional effects on dingoes, is to carry out detailed analyses of the parts of the anatomy involved in feeding, such as the cranial and jaw regions. Since traditional morphometrics has difficulty detecting introgression (Crowther *et al.* 2014, Elledge *et al.* 2008, Elledge *et al.* 2006, Newsome and Corbett 1982, Newsome *et al.* 1980), 3-D geometric morphometric approaches have been used to examine the impacts on the phenotypes of dingoes (Parr *et al.* 2016). In a geometric morphometric analysis, Parr *et al.* (2016) CT-scanned a total of 40 dingo, dingo with some dog ancestry, and dog skulls. Of the 14 wild caught pure dingoes, 11 were defined as pure in Newsome and Corbett (1982) due to the remote locations the specimens were collected and discriminant functions analysis of cranial measurements. The remaining three wild caught pure dingoes were identified based on microsatellite analysis (Wilton 2001, Wilton *et al.* 1999). Of the nine wild-caught dingoes with substantial domestic dog ancestry, six were defined as “hybrids” by Newsome and Corbett (1982) based on proximity to farms and on discriminant functions analysis of cranial measurements, and three wild-caught dingoes were confirmed as having substantial domestic dog ancestry by microsatellite testing (Wilton *et al.* 1999). There were also five F1 dingo × domestic dog hybrids from laboratory breeding experiments (Newsome and Corbett 1982). The remaining skulls were from dogs, twelve “pure-bred” dog skulls and five skulls from “cross-bred” domestic dogs. Dogs were chosen to represent the

dog breed in cases for which there were F1 dingo/dog × dog breed hybrids (kelpie, cattle dog, German shepherd, labrador) as well as greyhounds that are known to occur in rural Australia (Parr *et al.* 2016).

A principal components analysis of the landmarks revealed no separation of the dingoes and dingo-dog hybrids, regardless of the amount of domestic dog introgression (Parr *et al.* 2016 and Figure 1). PC1 describes 33.1 % of the variance in shape and reflects shape differences in the rostral length, zygomatic arch width, sagittal crest definition and the dorsal bossing of the anterior olfactory region of the cranium. PC2 describes an additional 20.7 % of variance in shape, with specimens scoring positively having lower, posterior parts of the olfactory region, a more dorsally angled rostrum, a more posteriorly pronounced sagittal crest and more posteriorly positioned occipital condyle and temporal mandibular joint. Dingoes with different levels of introgression overlap completely along PC2, showing no population differentiation. Domestic dogs were scattered throughout multivariate space, particularly along PC1, showing no natural groupings. Therefore, Parr *et al.* (2016) argued that domestic dog introgression does not affect dingo functional cranial morphology. This is not surprising, as wild type-recessive crosses often display the wild type morphology in the offspring (Leary and Allendorf 1989) and domestic dog phenotypic diversity has been maintained by continuously selecting for derived and recessive traits by dog breeders. Dingoes rely on their “wild-type” morphology to survive in natural conditions whereas domestic dogs have no need for such a constrained morphology. This could explain the limited presence of feral domestic dog populations with no dingo ancestry in Australia (Stephens *et al.* 2015) and why there are few or no established populations of feral dogs in Tasmania (Smith *et al.* 2019), where dingoes were never introduced (Letnic *et al.* 2014).

There is preliminary research indicating that introgression of domestic dog genes appears to have limited effects on the reproductive biology of the dingo. According to one study of 22 female dingoes of varying domestic dog ancestry, dingoes with domestic dog ancestry breed annually like dingoes rather than biannually like domestic dogs (Cursino *et al.* 2017). However, dingoes with higher levels of dog ancestry tended to have larger litter sizes (Cursino *et al.* 2017), hence more research is required on how introgression may affect dingo reproduction and potentially population dynamics.

Ecological effects of introgression in the dingo

There is extensive literature of the impacts of apex predators on ecosystems (Estes *et al.* 2011, Ripple *et al.* 2014), and this includes the dingo (Letnic *et al.* 2012). Dingoes suppress large herbivores (macropodids) and mesopredators (foxes and cats), and indirectly support

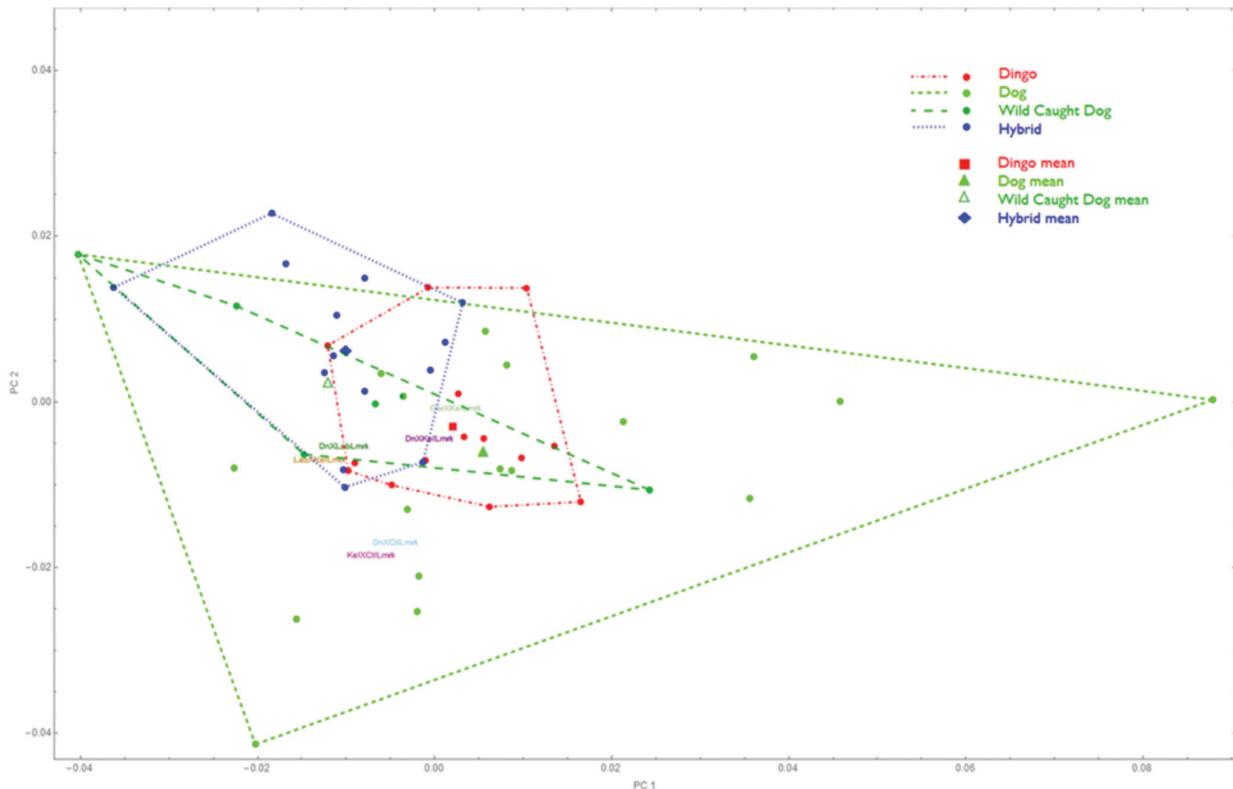


Figure 1: Plot of Principal Component (PC) axes 1 and 2 based on landmark measurements of dog and dingo skulls with different levels of dog introgression. First two axes represent 53.8% of the variation in the dataset. Figure reproduced from Parr *et al.* (2016)

growth of vegetation and small mammal numbers and diversity in arid (Brook *et al.* 2012, Gordon *et al.* 2017, Letnic and Crowther 2013, Letnic *et al.* 2009, Letnic and Koch 2010, Letnic *et al.* 2009), temperate mesic (Colman *et al.* 2015, Colman *et al.* 2014, Johnson and VanDerWal 2009) and tropical (Leo *et al.* 2019) environments (summarised in Figure 2). Although most of these studies are based on “mensurative” experiments in response to the dingo fence or baiting regimes, there is also recent manipulative experimental evidence of dingoes suppressing kangaroo and fox numbers while facilitating small mammals (Moseby *et al.* 2019).

Although there are no direct comparisons of “pure dingoes” with those with significant domestic dog ancestry on ecological impacts, the studies of ecosystem effects of dingoes are of populations with different levels of introgression. Introgression of domestic dog genes is low in arid Australia (Newsome *et al.* 2013, Stephens *et al.* 2015), and tropical northern Australia (Stephens *et al.* 2015) but in south-eastern Australia, introgression of domestic dog genes is relatively high (Cairns *et al.* 2020, Stephens *et al.* 2015), albeit with some geographical hotspots of low domestic dog ancestry (Cairns *et al.* 2020). In all areas of Australia, dingoes appear to have similar magnitudes in their ecosystem-wide impacts (Colman *et al.* 2014, Leo *et al.* 2019, Letnic *et al.* 2009), summarised as metanalysis results in Figure 2, hence

levels of domestic dog introgression appear to have no effect on the ecological role of the dingo.

Conclusion

Introgression is common across many species and is a part of the evolutionary process. Canids, with their 78 chromosomes and high phylogenetic relatedness, have had high levels of introgression in their evolutionary history. There has been extensive introgression of domestic dog genes into dingo populations, particularly in south-eastern Australia, since the European settlement of Australia. Persecution of dingoes with lethal control, which keeps dingo populations low and fractures social structures, may increase the risk of hybridisation, as has been suggested for introgression into wolf populations (Roy *et al.* 1994, Wayne and Jenks 1991). However, this introgression has had very little impact on some aspects of the functional morphology of dingoes. Ecological studies of dingoes across Australia, with different levels of domestic dog introgression, show very similar positive effects of dingoes through suppression of large herbivores and invasive mesopredators, and supporting native vegetation and small mammal populations. Hence, introgression from domestic dogs does not appear to be a major threat to the phenotype or ecological role of the dingo. Accordingly, hybridisation and resultant introgression from domestic dog genes do not diminish the conservation status of the dingo.

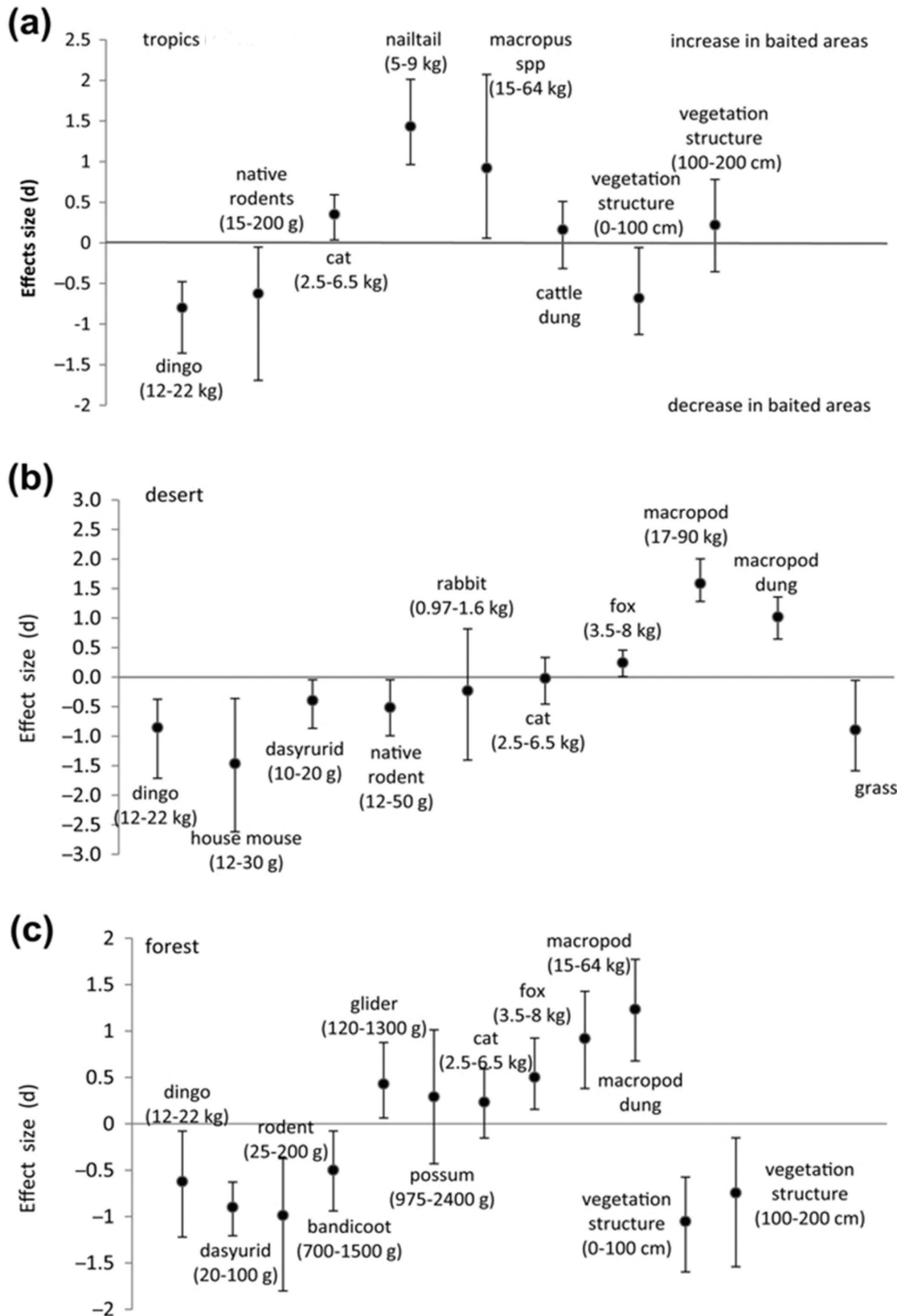


Figure 2: Effect sizes and confidence limits for (a) tropical and (b) arid (areas of low dog introgression) and (c) temperate (areas of high dog introgression) for the effects of dingoes on other parts of the ecosystem, including measurements on macropodids (kangaroos and wallabies), small mammals and vegetation. Hedge's *d* is the metric of effect size (Gurevitch and Hedges 1999), and all effects sizes below the 0 line represent a positive impact of dingoes, with those above the 0 line representing a negative impact of dingoes. Data from Leo et al. (2019), Letnic et al. (2009) and Colman et al. (2014)

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