An eco-evolutionary rationale to distinguish alien and native status: why the dingo is a native species on mainland Australia

Peter B. Banks

School of Life and Environmental Sciences, The University of Sydney, NSW 2006

ABSTRACT

Distinguishing between whether a species is alien or native can be problematic, especially for introduced species that are long-established in new areas outside of their natural range. Transport by humans is the criterion for alien status used by many definitions, whereas arbitrary time since arrival to a location is often used to define native status. Here I propose an eco-evolutionary approach to distinguish between alien and native status and use this to resolve uncertainty in the status of the dingo in Australia. Dingoes were transported to mainland Australia by humans, but more than 4000 years ago, and dingoes now interbreed with feral domestic dogs. Legally, this mix of events has the dingo classified as native in some jurisdictions and alien in others. I suggest that native status for introduced species should be based on (1) whether the species has evolved in their new environment; (2) whether local species recognise and respond to them as they do towards deep endemic native species, and; (3) whether their impacts benchmark against those of a native species or are exaggerated like those of other alien species. Dingoes are behaviourally, reproductively and morphologically different to close ancestors from south-east Asia, and this difference has a genetic basis indicative of evolution in Australia. There is abundant evidence that native prey species on mainland Australia recognise and respond to them as a dangerous predator, which they are. But there is strong evidence that dingo impacts on prey are not exaggerated, with effect sizes from mensurative experiments similar to those of experiments on native predators rather than alien predators. These three lines of evidence suggest dingoes should be considered native to mainland Australia. I suggest this eco-evolutionary approach to defining native status can be helpful in resolving the often-heated debates about when an alien species becomes native.

Key words: alien species, *Canis familiaris, Canis dingo*, domestic dog, invasive alien species, native species.

DOI: https://doi.org/10.7882/AZ.2021.039

Introduction

The definitions of what makes a species native or alien remains a major point of conjecture in ecology and conservation (Essl *et al.* 2018). For most deep endemic species (i.e. species with high levels of taxonomic endemism to a location (Walker *et al.* 2020) there is little argument about native status. But for those species that have moved outside their traditional range, there is significant concern about how they may affect the ecosystems that they invade, and such species are classically defined as alien (Essl *et al.* 2018). However, the movement of species has been occurring for millennia, including many species moved by humans (see summary of accounts by Chew 2011). These species don't neatly fit into easy definitions of being native, and call into question exactly how we define what is native and what is alien (Crees and Truvey 2015). In this paper I set out a framework for how conservation biology should define alien species ecologically, by examining as a case study the eco-evolutionary history of dingoes and their impacts on wildlife in Australia.

The dingo is considered by many to be Australia's native dog (Ritchie *et al.* 2018) and a natural and essential feature of the Australian environment but its status as a native species is not so certain. It is currently considered native in most state and federal legislation, which set various cut-off dates for a species to be considered native in Australia. Given the dingo's arrival more than 4000 years ago (Fillios and Taçon 2016) this date-based definition of nativeness makes the dingo distinct from the multitude of other novel species brought to Australia since 1788 (Long 2003). However, in 2018 the West Australian Government determined that the dingo could not be considered 'fauna', specifically native fauna, due to the extent of hybridisation between 'the dingo' and wild dogs. This decision shone a spotlight on the status of the dingo in Australia and re-opened old controversies about whether the dingo is a native species. It prompted an open letter to the Commonwealth Minister for the Environment from 25 dingo researchers from Australia and abroad (as well as an article in *Science,* Ritchie *et al.* 2018) arguing why the dingo is a native species, largely on the grounds of its taxonomic distinctiveness from domestic dogs. But being different to more recent arrivals does not confer native status *per se*.

Alien status certainly matters in conservation. Species considered alien in their ecosystems are typically targets for control and eradication whereas species considered native are most often protected (Chew and Hamilton

2011). Species that are classified as native are largely protected throughout Australia (at least the terrestrial vertebrates) and can receive conservation effort to sustain their populations. In general, they cannot be harmed, which includes trapping or killing, without a licence. They are valued by society. In contrast, species that are declared alien can usually be killed without concern about population-level impacts. If an alien species is declared vermin there is an obligation for population control and captured individuals cannot be released without a special licence. This distinction is exemplified in concern over the change of status of dingoes in Western Australia from fauna (i.e. native) to not fauna (i.e. non-native; Ritchie *et al.* 2018).

At the 1999 Royal Zoological Society of New South Wales symposium on the Dingo, Dickman and Lunney (2001) asked a simple question of the dingo: "Is it an Australian species and does it matter?" In this paper, 20 years on, I revisit the core issue at the heart of this question and answer it with an eco-evolutionary framework backed up with evidence for why dingoes should be considered native to mainland Australia, and domestic dogs probably should be too. Debate over the taxonomic distinctiveness of dingoes and dogs is still live and I do not consider it here, except to note that one school of thought holds that the scientific name is *Canis dingo* (Smith *et al.* 2019) and the other holds that the name is *Canis familiaris* (Jackson *et al.* 2021). Instead, I argue an ecological case for why the dingo is a native species to mainland Australia. In doing so I provide a general ecological approach to defining alien status.

A brief history of the native status of dingoes.

The debate over the nativeness of dingoes is long running (Dickman and Lunney 2001). Early consideration about the place of dingoes in Australia considered whether it was an indigenous species, i.e. *originating* in Australia rather than its native status per se. In his description of the species, Gould (1863) considered the dingo was not indigenous because it was brought to Australia by people. This definition aligns with many definitions of alien species (e.g. see Essl *et al.* 2018). Gould (1863) nonetheless quoted a letter from Gerard Krefft who, in contrast, considered the dingo to be an "original inhabitant of Australia" and in the Introduction to the *Mammals of Australia*, Gould highlighted that the dispute over native status revolved about whether humans brought dingoes to Australia. Interestingly, Gould never questioned the indigenous status of other placental mammals in Australia, such as rodents, and whether or not they "originated" in Australia. Like Krefft, Troughton (1962) also considered the dingo a native species but nevertheless asked whether the dingo, or native wild dog, evolved as an original inhabitant of the Australian continent. Corbett's (1995) seminal book "*The dingo in Australia and Asia*" also considered that the dingo was not indigenous to Australia as it did not "share an antiquity with the marsupial megafauna" but could nevertheless be considered a native species. Amongst these early arguments are implied concerns that having been brought to Australia by humans, the dingo cannot be a native species because it hasn't evolved in Australian systems, unlike marsupials.

More recent discussion over native status and dingoes has considered whether they are native or feral (Hytten 2009). These ideas also feature in debate of whether dingoes and dogs are distinct species (e.g. Jackson *et al.* 2017, 2021; Smith *et al.* 2019). In their *Field Guide to the Mammals of Australia*, Menkhorst and Knight (2004) list it with other Introduced Carnivores; Long's (2003) *Introduced Mammals of the world*, also lists the dingo with other feral dogs; Low (2002) argued the dingo is exotic regardless of when it arrived because it was brought here by people; Steve Van Dyck is quoted in Hytten 2009 as saying "Australia's so called native dog isn't native at all" and it should be sent back to where it came from. In these arguments the introduction of dingoes by humans continues to be the overriding consideration why the dingo cannot be considered native.

The lingering concern over hybridisation between dingoes and feral domestic dogs has also shaped debate over the dingo's native status, which for some authors depends upon its genetic purity and distinctiveness from domestic dogs (Hytten 2009, Probyn-Rapsey 2015). Corbett (1995) and many others considered the dingo at risk of extinction due to hybridisation with dogs although recent work suggests hybridisation is less widespread than previously thought (Cairns *et al.* 2020).

An eco-evolutionary approach to defining alien and native status for introduced species

i propose three staged elements in considering whether species that have moved to new places might be considered native: evolution, adaption and impact (Figure 1). These staged elements relate to their ecological impacts and the underlying evolutionary processes that shape them. They are implicit in many of the current ways that we define nativeness (e.g. time since arrival) and draw upon other work detailing the basis for concern about why alien species have negative impacts (e.g. Saul and Jenscke 2015) but do not seem to have been made explicit elsewhere. The approach here builds upon earlier ideas in Carthey and Banks (2012) who asked, "when does an alien species become a native?". Notably, a human role in moving the organism to a new location, which has been the source of much contention around past efforts to distinguish alien and native species (Gilroy et al. 2016), is not an essential part of the approach I propose here. Instead I focus on why conservation biology is concerned about alien species.

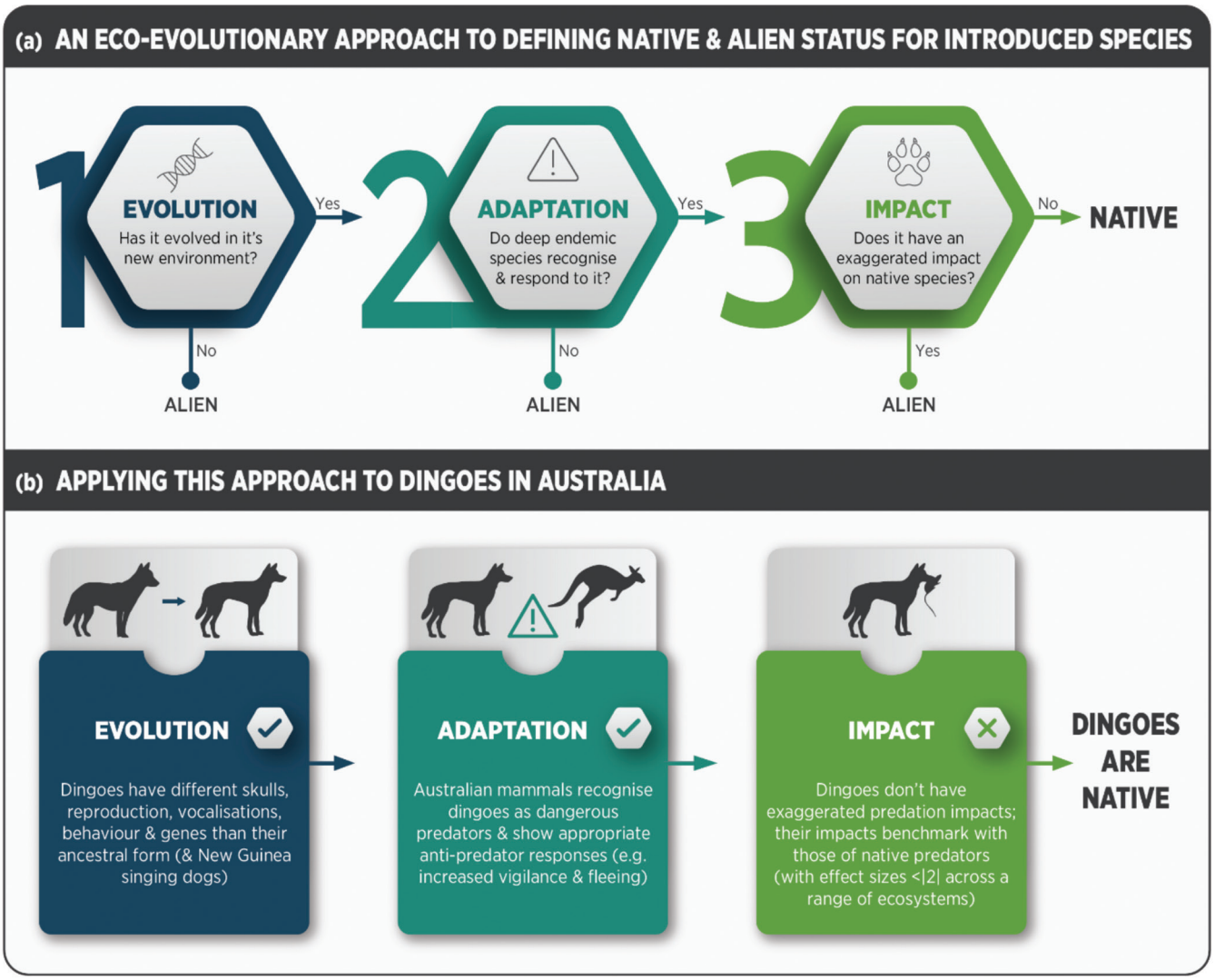

Figure 1: (a) An eco-evolutionary approach considering evolution of the species, adaptation in local species and impact on local species to distinguishing between native and alien status for introduced species; and (b) applying this approach to the status of dingoes in Australia.

1. Alien species lack evolution in their new environments

A core reason for concern about alien species is that they are new to the ecosystems that they invade, which means they haven't undergone extensive evolution in their new ecosystem (Saul and Jenscke 2015). They cannot be so mismatched that invasion will not succeed, but in arriving to a new location these non-resident species will have eco-evolutionary experiences and adaptions that have developed in other places. However, a lack of eco-evolution won't last long as there will be strong selective pressures from the new environment on individual fitness to drive phenotypic and evolutionary change (Cox 2004, Sax *et al.* 2007, Sih *et al.* 2011). There is abundant evidence that species introduced to new environments evolve adaptations that make them better suited to their new habitats (Shine 2012). For example, in Australian systems, cane toads *Rhinella marina* at the invasion front are morphologically, physiologically and genetically different from those that established in areas <100 years earlier (see summary by Rollins *et al.* 2015). This is just one example of many, showing that species that have moved to new locations adapt to their new environment.

2. Alien species have mismatches in interactions with residents

Alien species do novel things in their novel ecosystems largely because of mismatches in their interaction with local species. This will be caused by a mismatch in their eco-evolutionary experience and that of resident species (Saul and Jenscke 2015), that is, a lack of adaptation. For example, differences in information use or recognition can give one species an advantage over others (Sih *et al.* 2011) and such naïveté towards novel predators is thought to be a main reason why alien predators have exaggerated impacts (Salo *et al.* 2007). For example, failure by prey to recognise predators or the risks they pose give novel predators an advantage in the interaction (Bytheway *et al.* 2016). In contrast, the behavioural responses of predators

and prey that share a long history of coexistence results in no species having an ultimate advantage over the other (Abrams 2000). The anti-predator tactics used by prey make them difficult for predators to capture, especially when prey are rare, and not worth the search effort, resulting in Type 3 functional responses by predators that allow predator prey co-existence. When prey are naive, novel predators can show Type 2 functional responses that can more easily lead to prey extinction (Dick *et al.* 2017).

3. Alien species have alien, exaggerated impacts

Exaggerated ecological impacts are at the core of conservation concerns about alien species. Alien species are listed as the third greatest future threat to native biota after habitat loss and hunting (Tilman *et al.* 2017). They are part of Diamond's (1989) evil quartet of global extinction forces. Alien species, especially alien predators, are linked to the extinction or decline of dozens of species (Belllard *et al.* 2016). These rates of extinction linked to alien species are unusually high and well-beyond background levels (Blackburn *et al.* 2019). Salo *et al.* (2007) quantified the exaggerated nature of alien predator impacts by comparing effect sizes of alien vs native predator removal experiments. Removing an alien predator had double the effect size as removing native predators, across both replicated and unreplicated experiments. That is, while predation has an impact on prey, alien predators have an exaggerated impact. It is this exaggerated, unusual impact of alien species that defines the conservation dimension of their alienness. This logic only applies to long-established introduced species. For example, a lack of exaggerated impact on deep endemic local species by a recently arrived introduced species at low densities wouldn't meet native criteria without evidence of its evolutionary change and adaption in locals.

Alien status cannot be forever

Under classic definitions (e.g. Blackburn *et al.* 2014, Essl *et al.* 2018) alien status is forever: once a species is moved to a new location and becomes alien, that status is irreversible, unlike native status which can change (Chew and Hamilton 2011). Recently, Russell and Blackburn (2017) proposed two terms to describe introduced species that shouldn't be used interchangably; "alien" and "invasive alien" to identify concern over the significant negative impacts of some (invasive) species, yet both still forever remain alien species. However, changes to the eco-evolutionary experience of alien and resident species will mean that in time the impacts of once alien species will eventually change too (Strayer *et al.* 2006). For example, given the strength of selection imposed by predation (Vermeij 1982), there is likely to be strong selective pressure for recognition and response towards novel predators. Banks and Dickman (2007) suggested that naïveté towards novel predators changes over time and undergoes stages of improving recognition and response, transitioning from a lack of recognition of a novel enemy to strategies that are effective against exaggerated impacts.

Why the dingo is native to mainland australia

using the framework above, below I examine whether the dingo meets the definition of an alien species under the three elements of evolution, adaption and impact (Figure 1).

1. Dingoes have undergone evolution in Australia since introduction

There is little debate that the dingo is different from other closely related dogs with which it shares a common ancestor. Smith *et al.* (2019) summarise the evidence for how dingoes represent a distinct grouping of morphological, behavioural and reproductive traits, even though these traits are often shared with the enormous variety of domestic dog traits (Jackson *et al.* 2017, 2021). Compared to their closest ancestor, New Guinea Singing Dogs (Cairns 2021) dingoes have different-shaped skulls, differences in reproductive traits, different vocalisations and genetic differences (Smith *et al.* 2019). Zhang *et al.* (2020) recently identified changes in 13 genes linked to the feralization of the domestic ancestor of dingoes in south-east Asia. Presumably, these differences are the result of natural selection on dingoes in Australian environments in the 4000 years or so since their introduction (Zhang *et al.* 2020), rather than a stamp of domestication by people (Ballard and Wilson 2019). There is of course significant debate whether there has been enough change in dingoes to warrant status as a new species (e.g. see Jackson *et al.* 2021) but this question is not relevant here. Given the significant body of evidence of evolution in other alien species over shorter time frames (e.g. see review by van Kleunan *et al.* 2018), that dingoes would have undergone such natural selection in the Australian environment is uncontroversial. Evolutionary change is the first step towards native status.

2. Dingoes are recognised as a dangerous predator by native prey species

There is strong evidence that deep endemic Australian prey species recognise dingoes as predators and show appropriate anti-predator responses likely to be the result of adaptation. A meta-analysis of native prey responses to native and introduced vertebrate predators in Australia (Banks *et al.* 2018) found that 83% of studies of native marsupial and placental mammals showed prey recognition of dingo cues (sounds and odours). Moreover, these prey species adopted responses that are consistent with predator avoidance tactics (Banks *et al.* 2018), and similar to the responses they showed to cues of native marsupial predators (Figure 2). In response to cues from dingoes, Australian mammals are more vigilant, feed less,

and flee earlier (see review by Banks *et al.* 2018). Dingoes and domestic dogs were not distinguished as separate species in the meta-analysis because uncertain levels of hybridisation meant it was impossible to identify studies involving only "pure" dingoes.

Notably, it was only Australian mainland prey that consistently recognised dingoes/dogs as dangerous. For example, long nosed bandicoots in peri-urban Sydney were observed by residents much less often in backyards with dogs than those without (Carthey and Banks 2012). The same study, replicated in Hobart, Tasmania, where dingoes have never occurred, found that bandicoots showed no avoidance of yards with dogs (Frank *et al.* 2016). Together these results strongly support the hypothesis that bandicoots, like other native species in Australia, have evolved recognition of dingoes after >4000 years of coexistence. This is the second step in evolution towards nativeness.

3. Dingoes don't have exaggerated impacts on other native species

Alien species by definition have alien impacts, and for alien predators this mean exaggerated impact on their prey. Salo *et al.* 's (2007) meta-analysis of predation experiments showed that although native predators consistently suppress prey, alien predators had twice the impact on native prey as native predators. This result effectively benchmarked the exaggerated impacts of alien predators (mean effect size for predator removal experiments of 1.99) compared to native ones (mean effect size 0.65) which is thought largely due naïveté in local prey. Such processes can lead to exaggerated rates of extinction too (Blackburn *et al.* 2019). The approach has been used to benchmark impacts of introduced black rats *Rattus rattus* in bushland in peri urban Sydney that prey upon native skinks and suppress skink populations. Black rat impacts benchmark with those of native predators not alien predators, likely because skinks are also preyed upon by native rats (Smith *et al.* 2017) so that the degree of eco-evolutionary mismatches of skinks and rats was small. Given that dingoes and local prey have had up to 4000 years of shared evolutionary history and local prey consistently show recognition and anti-predator responses towards dingoes, simple naïveté, and hence exaggerated impacts, seem now unlikely.

Estimates of the impact of dingo predation support this idea and strongly suggest dingoes now function as a native predator in Australian ecosystems rather than as an alien predator. There have been no replicated experimental manipulations of dingo abundance to quantify their impacts on native prey (but see Moseby *et al.* 2019), and although some predator removal experiments using 1080 to control foxes *Vulpes vulpes* have also killed dingoes, these don't pinpoint dingo impacts. There have also been many mensurative studies used to estimate dingo impact, for example comparing prey abundance on either side of the dingo fence or in response to baiting regimes allowing estimates of effect size (e.g. Letnic *et al.* 2009, also summarised in Crowther *et al.* 2021). For every effect size measured, the impact of dingo predation benchmarks with those of the average native predator rather than an alien predator, with effect sizes <2 (and mostly <1) across a range of ecosystems (Figure 3). These analyses strongly suggest dingoes do not have the exaggerated impacts typical of alien species and dingo removal doesn't lead to very large prey population increases that typically follow removal

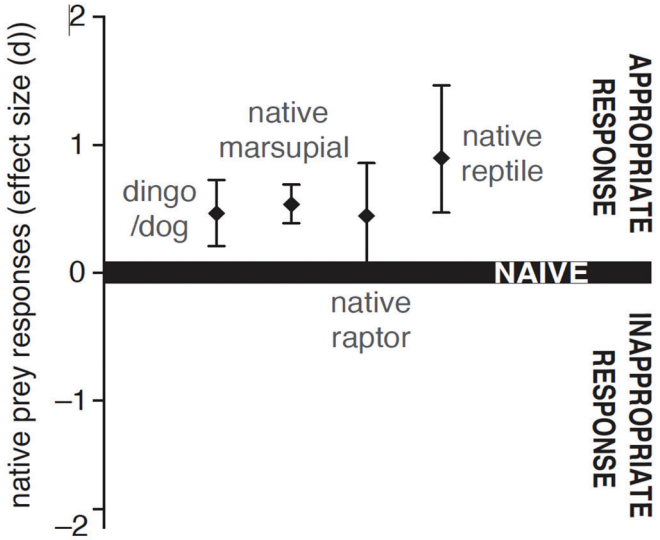

Figure 2: Results of a meta-analysis (adapted from Banks *et al.* 2018) showing the deep endemic native prey show recognition and appropriate anti predator responses towards dingoes/dogs, similar to the responses shown towards native marsupial, reptile and bird predators

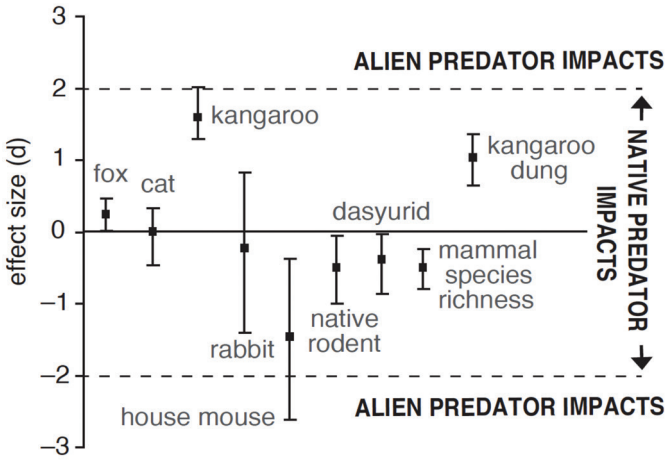

Figure 3: Excluding dingoes (via dingo fence) reveals impacts on prey with effect size < |2| (figure adapted from Letnic *et al.* 2009), which is typical of native predator exclusion. In contrast, the effect size of alien predators is > |2| .

of an alien predator (Salo *et al.* 2007). In contrast, for example, experimental removals of foxes result in effect sizes for Australian native prey of 2.07-4.80 (Salo *et al.* 2007). Notably though, for some smaller native species, it is possible that the impact of dingo exclusion might be tempered by consequence increases in impacts of introduced mesopredators (Letnic *et al.* 2012), although small mammals are not often a major part of the dingo diet (see review by Doherty *et al.* 2019).

There is indirect evidence that dingoes sometimes have exaggerated impacts on native prey, although the evidence is more qualitative than the quantitative evidence available for more recently introduced predators such as cats *Felis catus* (McGregor *et al.* 2015) and foxes (Short *et al.* 2002). Allen and Fleming (2012) summarise several accounts of dingoes being linked to population declines of mammals. For instance, a single dingo killed 17 burrowing bettongs in a few days, but these were captive raised, predator naive individuals and dingo impact on established bettongs is not reported. Dingoes have also been linked to the steep decline of arid zone brush tailed possums (Kerle *et al.* 1992), but only after numbers were driven low by drought and disturbance to refuge. These individual accounts aren't necessarily inconsistent with accounts of other traditionally-defined native species becoming pests locally especially in human-modified environments. However, in contrast to these individual accounts, there is much evidence of coexistence between dingoes and prey on both sides of the dingo fence (see review by Crowther *et al.* 2021) and the weight of evidence would seem to favour dingoes having native rather than alien impacts on prey.

Dingo impacts on native species were probably not always so benign. Dingoes are linked to the extinction of Tasmanian devils *Sarcophilis harrisii*, Thylacines, also called Tasmanian Tigers *Thylacinus cynocephalus* and the Tasmanian flightless hen *Gallinula mortierii* which disappeared from mainland Australia with the arrival of the dingo. Questions have been asked whether such declines were due to co-incidental changes in human demographics (Johnson and Wroe 2003, Letnic *et al.* 2014), climate change (Prowse *et al.* 2014) or human hunting (Letnic *et al.* 2014). However, given the well documented accounts of the impacts on island fauna after introducing domestic dogs (Letnic *et al.* 2014, Doherty *et al.* 2017) and other alien species (Bellard *et al.* 2016), it is very possible there were exaggerated dingo impacts leading to extinction soon after their arrival to mainland Australia. I argue here that such impacts no longer occur because of evolutionary change in both dingoes and their prey.

Implications

Defining introduced species as native with this eco-evolutionary approach has several unsettling implications. Firstly, the lines of arguments I use here to define eco-evolutionary nativeness in dingoes also suggest that domestic dogs might be considered native on mainland Australia too, at least when outside of the influence of humans. In terms of evolution, domestic dog populations that have gone feral undergo evolutionary change, probably quite quickly (Zhang *et al.* 2020). In terms of prey naïveté, much of the evidence for native prey species responses to predation risk from dingoes involves samples taken from dingo/dog hybrids or domestic dogs- native prey don't seem to distinguish between the two (Banks *et al.* 2018). In terms of the extent of impacts, Crowther *et al.* (2021) show that the degree of introgression of dingo/dog hybridisation has little impact on the effect size of predation on native prey, none of which benchmarks as alien. Of course, predator numbers, whether dingoes or dogs, that are sustained by human resources can lead to exaggerated impacts on prey (Doherty *et al.*2 017). But given that prey don't seem to distinguish between domestic dogs and dingoes, and their impacts don't differ, both are probably native, at least by the eco-evolutionary definition proposed here. This makes arguments about a taxonomic distinction between dingoes and dogs somewhat moot.

Secondly, this definition doesn't align simply with geopolitical boundaries. An introduced species might meet the criteria for native status in one area of a country but not another. This is the case for dingoes being native on mainland Australia but not on islands. It can also be applied to "native" species that have moved to new environments within geopolitical boundaries where it is technically defined as native, but has the potential for significant impacts on local species (Campbell *et al.* 2018).

Thirdly this approach has clear implications for considerations of rewilding of once "native" species. For example, proposals (or guerrilla action) to release Tasmanian devils onto mainland Australia are typically framed around rewilding or even restoring a lost species (e.g. see Bode 2021). However, in the 3000 or so years since the devil's demise, evolution will have occurred in the devils in Tasmania as well as in the wildlife on the devil-free mainland. A lack of naïveté towards devils in local wildlife and lack of exaggerated impacts which define nativeness cannot be guaranteed. Indeed, recent release of devils on Maria Island had a devastating impacts on local seabirds (Scoleri *et al.* 2020).

Finally, species introduced into a new ecosystem eventually make many connections with local species, some of which may be positive ones too (cf. the complex pest, after Dickman 2007). Definitions of nativeness of a species should ideally factor in the full range of its interactions and impacts on local species, which is challenging for most species where there is limited evidence for their interactions or impacts. This is perhaps why rules of thumb like "time since introduction" is used to define nativeness, which remain useful when that timeframe is short.

Conclusion

Defining native status in a species is of course a human construct, but it has important implications to determine how humans interact with a species, and ultimately its fate. Past definitions of nativeness based on time since introduction, taxonomic distinctiveness (being different from more recent arrivals) or ecological role (e.g. eating native foods or playing an apex role) have been controversial (Essl *et al.* 2018). This may be because they haven't really tapped into exactly why conservation feels the need to identify some species as alien and the ecological mechanisms that underpin such identities. However, there is a well-founded notion that aliens are often bad for conservation, while natives are good (Brown and Sax 2005). The approach I propose here is not about giving up on managing alien species or adopting all species as native: introduced species should still be considered alien until proven native. The approach suggested here aims to determine what determines whether introduced species that have moved beyond their historic range many years ago are good or bad for conservation, in an eco-evolutionary sense. It helps to explain why we should consider dingoes (and probably domestic dogs) as native on mainland Australia (including in Western Australia) and should have application in many other systems to consider when alien species might be considered native.

Acknowledgements

The ideas behind the manuscript have been developed over the years from helpful discussions with Amelia Saul, Kyla Johnstone and Alex Carthey along with the BIOL2024 and ENVI7505 classes at the University of Sydney. I thank Amelia Saul, Jenna Bytheway, Catherine Price, Casey Taylor, Finn Parker, Patt Finnerty, Gabriel Orlando, Ben Reay and two anonymous reviewers for insightful comments on an earlier draft of this manuscript. Many thanks to Jenna Bytheway for creating the figures, including the infographic. The work was supported by an Australian Research Council Grant DP140104413.

References

Abrams, P.A. 2000. The evolution of predator-prey interactions: theory and evidence. *Annual Review of Ecology and Systematics* **31**: 79-105.

Allen, B.L. and Fleming, P.J.S. 2012. Reintroducing the dingo: the risk of dingo predation to threatened vertebrates of western New South Wales. *Wildlife Research* **39**: 35-50.

Ballard, J.W.O. and Wilson, L.A. 2019. The Australian dingo: untamed or feral? *Frontiers in Zoology* **16**:1-19.

Banks, P.B. and Dickman, C.R. 2007. Alien predation and the effects of multiple levels of prey naiveté. *Trends in Ecology & Evolution* **22**: 229-30.

Banks, P.B., Carthey, A.J. and Bytheway, J.P. 2018. Australian native mammals recognize and respond to alien predators: a meta-analysis. *Proceedings of the Royal Society B* **285**, p.20180857.

Bellard, C., Cassey, P. and Blackburn, T.M. 2016. Alien species as a driver of recent extinctions. *Biology Letters* **12**, p.20150623.

Blackburn, T.M., Bellard, C. and Ricciardi, A. 2019. Alien versus native species as drivers of recent extinctions. *Frontiers in Ecology and the Environment* **17**: 203-207.

Bode, M. 2021. Covert rewilding: Modelling the detection of an unofficial translocation of Tasmanian devils to the Australian mainland. *Conservation Letters* **14**, p.e12787.

Brown, J.H. and Sax, D.F. 2005. Biological invasions and scientific objectivity: reply to Cassey *et al.* (2005). *Austral Ecology* **30**: 481-483.

Bytheway, J.P., Price, C.J. and Banks, P.B. 2016. Deadly intentions: naïve introduced foxes show rapid attraction to odour cues of an unfamiliar native prey. *Scientific Reports* **6**: 1-6.

Cairns, K.M., Nesbitt, B.J., Laffan, S.W., Letnic, M. and Crowther, M.S. 2020. Geographic hot spots of dingo genetic ancestry in southeastern Australia despite hybridisation with domestic dogs. *Conservation Genetics* **21:** 77-90.

Cairns, K.M. 2021. What is a dingo–origins, hybridisation and identity. *Australian Zoologist* **41**: 322-337. https://doi.org/10.7882/AZ.2021.004

Campbell, C.D., Sarre, S.D., Stojanovic, D., Gruber, B., Medlock, K., Harris, S., MacDonald, A.J. and Holleley, C.E. 2018. When is a native species invasive? Incursion of a novel predatory marsupial detected using molecular and historical data. *Diversity and Distributions* **24**: 831-840.

Carthey, A.J. and Banks, P.B. 2012. When does an alien become a native species? A vulnerable native mammal recognizes and responds to its long-term alien predator. *PloS one* **7**: p.e31804.

Chew, M.K. and Hamilton, A.L. 2011. The rise and fall of biotic nativeness: a historical perspective. Pp 35-48 in *Fifty years of invasion ecology: the legacy of Charles Elton*, edited by D.M Richardson), Wiley-Blackwell, West Sussex

Chew, M.K. 2011. Invasion biology: historical precedents. Pp. 369-375 in *Encyclopaedia of biological invasions,* edited by D. Simberloff and M Rejmánek, University of California Press.

Corbett, L.K. 1995. *Dingo in Australia and Asia*. UNSW Press, Kensington.

Cox, G.W. 2004. *Alien species and evolution: the evolutionary ecology of exotic plants, animals, microbes, and interacting native species*. Island Press, Washington.

Crees, J.J. and Turvey, S.T. 2015. What constitutes a 'native' species? Insights from the Quaternary faunal record. *Biological Conservation* **186**:143-148.

Crowther, M.S., Cairns, K.M., van Eeden, L.M. and Letnic, M. 2021. Introgression does not influence the positive ecological and functional role of dingo populations. *Australian Zoologist* **41**: 338-346. https://doi.org/10.7882/AZ.2020.016

Diamond, J. M. 1989. Overview of recent extinctions. Pp. 37-41 in *Conservation for the Twenty-first Century*, edited by D. W. Western & M. C. Pearl, Oxford University Press, Oxford, UK.

Dick, J.T., Laverty, C., Lennon, J.J., Barrios-O'Neill, D., Mensink, P.J., Robert Britton, J., Médoc, V., Boets, P., Alexander, M.E., Taylor, N.G. and Dunn, A.M. 2017. Invader Relative Impact Potential: a new metric to understand and predict the ecological impacts of existing, emerging and future invasive alien species. *Journal of Applied Ecology* **54:** 1259-1267.

Dickman, C.R. and Lunney, D. 2001. Last howl of the dingo: the legislative, ecological and practical issues arising from the kill-or-conserve dilemma. Pp 95-107 in *A Symposium on the Dingo*, edited by C.R. Dickman and D Lunney, Royal Zoological Society of New South Wales, Mosman.

Dickman, C. R. 2007. The complex pest: interaction webs between pests and native species. Pp. 208-215 in *Pest or Guest: The Zoology of Overabundance*, edited by D. Lunney, P. Eby, P. Hutchings and S. Burgin. Royal Zoological Society of New South Wales: Mosman, Australia.

Doherty, T.S., Dickman, C.R., Glen, A.S., Newsome, T.M., Nimmo, D.G., Ritchie, E.G., Vanak, A.T. and Wirsing, A.J. 2017. The global impacts of domestic dogs on threatened vertebrates. *Biological Conservation* **210**:56-59.

Doherty, T.S., Davis, N.E., Dickman, C.R., Forsyth, D.M., Letnic, M., Nimmo, D.G., Palmer, R., Ritchie, E.G., Benshemesh, J., Edwards, G. and Lawrence, J. 2019. Continental patterns in the diet of a top predator: Australia's dingo. *Mammal Review* **49**: 31-44.

Essl, F., Bacher, S., Genovesi, P., Hulme, P.E., Jeschke, J.M., Katsanevakis, S., Kowarik, I., Kühn, I., Pyšek, P., Rabitsch, W. and Schindler, S. 2018. Which taxa are alien? Criteria, applications, and uncertainties. *BioScience* **68:** 496-509.

Fillios, M.A. and Taçon, P.S. 2016. Who let the dogs in? A review of the recent genetic evidence for the introduction of the dingo to Australia and implications for the movement of people. *Journal of Archaeological Science: Reports* **7**: 782-792.

Frank, A.S., Carthey, A.J. and Banks, P.B. 2016. Does historical coexistence with dingoes explain current avoidance of domestic dogs? Island bandicoots are naïve to dogs, unlike their mainland counterparts. *PloS one* **11**: p.e0161447.

Gilroy, J.J., Avery, J.D. and Lockwood, J.L. 2017. Seeking international agreement on what it means to be "native". *Conservation Letters* **10**: 238-247.

Gould, J. 1863. *The Mammals of Australia-Vol. 3*. The Author, London.

Hytten, K. 2009. Dingo dualisms: Exploring the ambiguous identity of Australian dingoes. *Australian Zoologist* **35**: 18-27.

Jackson, Stephen M., Colin Groves, Peter JS Fleming, Ken P. Aplin, Mark DB Eldridge, Antonio Gonzalez, and Kristopher M. Helgen 2017. The wayward dog: Is the Australian native dog or dingo a distinct species? *Zootaxa* **4317**: 201–224.

Jackson, S.M., Fleming, P.J., Eldridge, M.D., Archer, M., Ingleby, S., Johnson, R.N. and Helgen, K.M. 2021. Taxonomy of the Dingo: It's an ancient dog. *Australian Zoologist* **41**:347-357. DOI: https://doi.org/10.7882/AZ.2020.049

Johnson, C. N., and S. Wroe 2003. Causes of extinction of vertebrates during the Holocene of mainland Australia: arrival of the dingo, or human impact?. *The Holocene* **13**: 941-948.

Kerle, J.A., Foulkes, J.N., Kimber, R.G. and Papenfus, D. 1992. The decline of the brushtail possum, *Trichosurus vulpecula* (Kerr 1798), in arid Australia. *The Rangeland Journal* **14**: 107-127.

Letnic, M., Fillios, M. and Crowther, M.S. 2014. The arrival and impacts of the dingo. Pp 53-67 in *Carnivores of Australia: past, present and future*, edited by A. Glen and C.R. Dickman. CSIRO Publishing, Melbourne.

Letnic, M., Koch, F., Gordon, C., Crowther, M.S. and Dickman, C.R. 2009. Keystone effects of an alien top-predator stem extinctions of native mammals. *Proceedings of the Royal Society B: Biological Sciences* **276**: 3249-3256.

Letnic, M., Ritchie, E.G. and Dickman, C.R. 2012. Top predators as biodiversity regulators: the dingo *Canis lupus dingo* as a case study. *Biological Reviews* **87**: 390-413.

Long, J.L. 2003. *Introduced mammals of the world: their history, distribution, and influence*. CSIRO Publishing.

Low, T. 2002. *Feral future: the untold story of Australia's exotic invaders*. University of Chicago Press.

McGregor, H., Legge, S., Jones, M.E. and Johnson, C.N. 2015. Feral cats are better killers in open habitats, revealed by animal-borne video. *PloS one* **10**: p.e0133915.

Menkhorst, P. and Knight, F. 2004. *Field guide to the mammals of Australia*. Oxford University Press.

Moseby, K. E., Crowther, M. S. and Letnic, M. 2019. Ecological role of an apex predator revealed by a reintroduction experiment and Bayesian statistics. *Ecosystems* **22**: 283-295.

Probyn-Rapsey, F. 2015. Dingoes and dog-whistling: A cultural politics of race and species in Australia. *Animal Studies Journal* **4**: 55-77.

Prowse, T.A., Johnson, C.N., Bradshaw, C.J. and Brook, B.W. 2014. An ecological regime shift resulting from disrupted predator–prey interactions in Holocene Australia. *Ecology* **95**: 693-702.

Ritchie, E., Smith, B.P., Van Eeden, L.M. and Nimmo, D.G. 2018. Species definitions shape policy. *Science* **361**: 1324-1324.

Rollins, L.A., Richardson, M.F. and Shine, R. 2015. A genetic perspective on rapid evolution in cane toads (*Rhinella marina*). *Molecular Ecology* **24**: 2264-2276.

Russell, J.C. and Blackburn, T.M. 2017. Invasive alien species: denialism, disagreement, definitions, and dialogue. *Trends in Ecology & Evolution* **32**: 312-314.

Salo, P., Korpimäki, E., Banks, P.B., Nordström, M. and Dickman, C.R. 2007. Alien predators are more dangerous than native predators to prey populations. *Proceedings of the Royal Society B: Biological Sciences* **274**: 1237-1243.

Saul, W.C. and Jeschke, J.M. 2015. Eco-evolutionary experience in novel species interactions. *Ecology Letters* **18:** 236-245.

Sax, D.F., Stachowicz, J.J., Brown, J.H., Bruno, J.F., Dawson, M.N., Gaines, S.D., Grosberg, R.K., Hastings, A., Holt, R.D., Mayfield, M.M. and O'Connor, M.I. 2007. Ecological and evolutionary insights from species invasions. *Trends in Ecology & Evolution* **22**: 465-471.

Sax, D.F., Stachowicz, J.J., Brown, J.H., Bruno, J.F., Dawson, M.N., Gaines, S.D., Grosberg, R.K., Hastings, A., Holt, R.D., Mayfield, M.M. and O'Connor, M.I. 2007. Ecological and evolutionary insights from species invasions. *Trends in Ecology & Evolution* **22**: 465-471.

Scoleri, V.P., Johnson, C.N., Vertigan, P. and Jones, M.E. 2020. Conservation trade-offs: Island introduction of a threatened predator suppresses invasive mesopredators but eliminates a seabird colony. *Biological Conservation* **248**: p.108635.

Shine, R. 2012. Invasive species as drivers of evolutionary change: cane toads in tropical Australia. *Evolutionary Applications* **5**: 107-116.

Short, J., Kinnear, J.E. and Robley, A. 2002. Surplus killing by introduced predators in Australia—evidence for ineffective anti-predator adaptations in native prey species?. *Biological Conservation* **103:** 283-301.

Sih, A., Ferrari, M.C. and Harris, D.J. 2011. Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications* **4**: 367-387.

Smith, B. P., Cairns, K. M., Adams, J. W., Newsome, T. M., Fillios, M., Deaux, E. C., Parr, W. C. H., Letnic, M., Van Eeden, L. M., Appleby, R. G., Bradshaw, C. J. A., Savolainen, P., Ritchie, E. G., Nimmo, D. G., Archer-lean, C., Greenville, A., Dickman, C. R., Watson, L., Moseby, K. E., Doherty, T. S., Wallach, A. D., Morrant, D. S. and Crowther, M. S. 2019. Taxonomic status of the Australian dingo: the case for *Canis dingo* Meyer, 1793. *Zootaxa* **4564**: 173-197

Smith, H.M., Dickman, C.R. and Banks, P.B. 2017. Using effect size benchmarks to assess when alien impacts are actually alien. *Scientific Reports* **7**: 1-8.

Strayer, D.L., Eviner, V.T., Jeschke, J.M. and Pace, M.L. 2006. Understanding the long-term effects of species invasions. *Trends in Ecology & Evolution* **21**:645-651.

Tilman, D., Clark, M., Williams, D.R., Kimmel, K., Polasky, S. and Packer, C. 2017. Future threats to biodiversity and pathways to their prevention. *Nature* **546**: 73-81.

Troughton, E. 1962. *Furred Animals of Australia*. Angus and Robertson, Sydney.

van Kleunen, M., Bossdorf, O. and Dawson, W. 2018. The ecology and evolution of alien plants. *Annual Review of Ecology, Evolution, and Systematics* **49:** 25-47.

Vermeij, G.J. 1982. Unsuccessful predation and evolution. *The American Naturalist* **120:** 701-720.

Walker, S., Monks, A. and Innes, J.G. 2021. Life history traits explain vulnerability of endemic forest birds and predict recovery after predator suppression. *New Zealand Journal of Ecology* **45**: p.3447.

Zhang, S.J., Wang, G.D., Ma, P., Zhang, L.L., Yin, T.T., Liu, Y.H., Otecko, N.O., Wang, M., Ma, Y.P., Wang, L. and Mao, B. 2020. Genomic regions under selection in the feralization of the dingoes. *Nature Communications* **11**: 1-10.