Chapter 4

Top-Predators as Biodiversity Regulators: Contemporary Issues Affecting Knowledge and Management of Dingoes in Australia

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1. Introduction

Large predators have an indispensable role in structuring food webs and maintaining ecological processes for the benefit of biodiversity at lower trophic levels. Such roles are widely evident in marine and terrestrial systems [1, 2]. Large predators can indirectly alleviate predation on smaller (and often threatened) fauna and promote vegetation growth by interacting strongly with sympatric carnivore and herbivore species (e.g. [3-5]). The local extinction of large predators can therefore have detrimental effects on biodiversity [6], and their subsequent restoration has been observed to produce positive biodiversity outcomes in many cases [7]. Perhaps the most well-known example of this is the restoration of gray wolves *Canis lupus* to the Greater Yellowstone Ecosystem of North America. Since the reintroduction of 66 wolves in 1995 [8], wolf numbers in the area have climbed to ~2000, some large herbivores and mesopredators have substantially declined, and some fauna and flora at lower trophic levels have increased (see [4], and references therein). Similar experiences with some other large predators mean that they are now considered to be of high conservation value in many parts of the world [1, 2, 7], and exploring their roles and functions has arguably been one of the most prominent fields of biodiversity conservation research in the last 10–15 years.

Large terrestrial predators are often top-predators (or apex predators), but not all top-predators are large or associated with biodiversity benefits [5, 9]. For example, feral cats *Felis catus* or black rats *Rattus rattus* may be the largest predators on some islands, but their effects on endemic fauna are seldom positive [10-13]. In geographically larger systems, coyotes (*Canis latrans*) [14] or dingoes (*Canis lupus dingo* and other free-roaming *Canis*) [15],

for example, can exacerbate wildlife management problems in highly perturbed ecosystems, where they have the capacity to devastate populations of smaller prey [5, 16-18]. Hence, it is not the trophic position of a predator that determines their ecological effects, but rather their behaviour, impact and function [9]. This is most important for small- and medium-sized predators which can have positive, negative or neutral effects depending on a range of context-specific factors.

Excluding humans, dingoes are the largest terrestrial predator on mainland Australia but, at an average adult body weight of only 15–20 kg [19], are atypical top-predators [20-22]. No other continent has such a small top-predator, and canids have rarely (if ever) been a continent's largest predator, a role typically filled by ursids or felids. Australia's former terrestrial top-predator, a similar-sized marsupial known as the thylacine or Tasmanian Tiger *Thylacinus cynocephalus*, was quickly replaced by dingoes as the largest predator as thylacines became extinct coincident with the introduction of dingoes to Australia about 4000–5000 years ago [23-25]. Like all dogs, dingoes are derived from wolves by human selection [26-29], yet it is a mistake to equate dingoes with wolves (*sensu* [30, 31]) simply because they share a common origin [9, 22, 32] and display some wolf-like behaviours [19]. Hence, the net effects of dingoes on biodiversity might not be readily deduced from studies of other top-predators. Regardless of their derivation and exotic origin, dingoes are common across most of Australia's mainland biomes [33, 34], although their densities have been reduced to very low levels in some regions (<25% of Australia) where sheep *Ovis aries* and goats *Capra hircus* are farmed [15, 34].

Dingoes can have neutral, positive or negative effects (which can be either direct or indirect) on economic, environmental and social values [22, 35]. For example, dingoes can adversely affect livestock production by preying on livestock [36, 37], yet have beneficial effects to livestock producers by preying on livestock competitors [38, 39]. Alternatively, dingoes might help to reduce the impacts of smaller predators (such as introduced red foxes *Vulpes vulpes* or feral cats) on threatened fauna through intraguild predation or exploitative competition [40, 41], yet have detrimental effects on the same fauna through predation [15, 16] and/or disease transmission [42, 43]. Human attitudes towards dingoes are also variable [22, 44-46]. Hence, it should not be surprising to discover evidence for diverse and contrasting functions and values of dingoes in different places and at different times, which adds complexity to their best-practice management [35].

Knowledge of the roles of top-predators on other continents (e.g. [1, 2]) and recent research focus on the positive environmental effects of dingoes (e.g. [41, 47, 48]) has led to calls to cease lethal dingo control (e.g. [31, 49]) and even restore them to sheep and goat production regions (e.g. [23, 50]), actions collectively referred to hereafter as 'positive dingo management'. Serious concerns about the validity and rigour of the science supporting positive dingo management have been raised (e.g. [15, 51, 52], but see also [33, 53, 54]). The issue is further complicated by the changing genetic identity of dingoes [55-58] and the associated ambiguity and misuse of taxonomic terminology ([33]; e.g. compare taxonomic nomenclature between [56], [59], [60], and [55]). The capacity for dingoes to exploit seemingly unsusceptible fauna [61] and the widespread and direct negative effects of

dingoes on biodiversity are also overlooked in many cases [15, 16]. There remains, however, a general view that dingoes provide net benefits to biodiversity at continental scales through suppression of foxes (Plate 1), feral cats and herbivores such as kangaroos (*Macropus* spp.) and rabbits (*Oryctolagus cuniculus*) [9, 47], and policy and practice recommendations towards positive dingo management are already occurring (e.g. [49, 62, 63]) despite concerns over the state of the literature and the conflicting roles of the dingo. In most places dingoes are presently managed on the basis of where they occur and what they are (or are perceived to be) doing, not on their genetics or appearance [33, 64].

Out of the confusion arise several knowledge gaps and issues which hamper the informed management of dingoes for biodiversity conservation. In this chapter we discuss critical knowledge gaps about dingo ecology, and highlight the influence of methodological application and design flaws on the reliability of published literature underpinning current knowledge of the ecological roles of dingoes. We offer alternative explanations for the mostly correlative data often mooted as 'clear and consistent evidence' (e.g. [54, 65]) for the fox-suppressive effects of dingoes, and discuss practical obstacles to the accrual of biodiversity benefits expected from positive dingo management. We also discuss the potential consequences of such a management approach for biodiversity and livestock industries, and the management of dingoes at scales which can address their context-specific impacts. Finally, we summarise some surmountable issues presently faced by researchers, land managers and policy makers, and provide recommendations for future research that, when completed, will assist in filling the knowledge gaps required to progress the best-practice management of dingoes for biodiversity conservation in Australia.

2. Knowledge gaps in the literature

Dingoes are one of the most studied animals in Australia, but there is still much to learn about them. Management of dingoes can be advanced by directing researchers towards critical knowledge gaps which require exploration. Unsurprisingly, some gaps need more urgent attention than others. Here, we focus on four key knowledge gaps that we consider to be fundamental to achieving best-practice management of dingoes as biodiversity conservation tools. These are:

1. The relationships between dingoes and biodiversity in relatively intact ecosystems
2. The relationships between dingoes and biodiversity in relatively altered ecosystems characterised by grossly disturbed vegetation structure and composition
3. The effects of current dingo control practices on mesopredators and biodiversity
4. The public's view of what we're trying to conserve (i.e. their pelage, their genetic identity and/or their ecological function)

Dingoes have been studied in many parts of Australia [19], but mostly in relatively intact (i.e. parks, reserves or extensive cattle production regions) and/or arid (Table 1) areas. This is mirrored by international research [2] that primarily comes from a limited number of classic studies conducted in relatively intact ecosystems that do not represent the majority of the earth's surface [66]. Although the relationships between dingoes and biodiversity in

these intact areas might be considered well studied, they are not well understood, because the majority of the literature addressing the ecological roles of dingoes in these areas is compromised by a variety of methodological flaws [52]. Even ignoring these flaws, the majority of the relevant literature is only observational and correlative [41], and is therefore subject to plausible alternative explanations [67, 68]. Key among these is the cumulative effects of pastoralism (e.g. [15, 53]), which dramatically transformed pre-European landscapes into those characterised by severely altered vegetation communities [69-71] and a high proportion of now rare and locally extinct native fauna [72-75]. Understanding the roles of dingoes in highly altered ecosystems (i.e. sheep grazing lands and urban ecosystems) may actually be most important, because such systems are those expected to benefit most from positive dingo management [23, 50].

Since the 1960s, when the modern era of dingo research began, most studies have focussed on basic biology, including dingo diet, pack structure, physiology and reproductive biology [19, 76]. The motivation for much of this work has been directed at the negative effects of dingoes on livestock production [19, 64], and dingoes are presently subject to lethal control in many places in attempts to alleviate livestock predation [32, 64, 77]. However, due to the recently reported positive roles of dingoes and other top-predators on biodiversity conservation [1, 2, 7], lethal dingo control has come under increased scrutiny over its perceived indirect effects on biodiversity (e.g. [49]); the idea being that dingo control leads to negative outcomes for faunal biodiversity through trophic effects [23, 78]. Noteworthy however, is that the predicted negative effects of dingo *control* on faunal biodiversity are largely only presumed, and have rarely been demonstrated [79]. Regardless, the conservation and encouragement of dingoes is still being advocated on biodiversity conservation grounds (e.g. [23, 76]). However, *what* exactly requires conservation has not yet been determined for dingoes, which are listed as threatened species [56, 63] not because they are rare (in contrast, there are probably more dingoes now than at any other time in Australia's ecological history [33]), but because their genetic identity is again being altered through hybridisation [55, 57]. Unfortunately, phenotype or pelage is an unreliable indicator of genetic purity [58, 80], though most lay people equate purity with pelage (where only a sandy-coloured dingo is assumed to be pure). Alternatively, it may not be their colour or genetic identity that requires conservation, but their ecological roles [76]. Identifying what is to be conserved is important because most dingoes in Australia are not pure and are expected to become less so with time [55-57].

Understanding the trophic relationships between dingo management practices (i.e. poison baiting, trapping, shooting or no human intervention at all) and the conservation of threatened prey species (R1–R6 in Fig. 1) is the most critical management challenge [22, 41]. A wide variety of taxa may be involved (Plate 1). Ecological relationships between organisms are rarely as simple as those described in Fig. 1, yet they are often assumed to be so in studies of dingoes [32]. The (mostly negative) relationships between exotic mesopredators and threatened prey species (R3) are relatively well understood from other studies [81, 82], as is the relationship between lethal dingo control and dingoes (R1) [64, 83]. The other two relationships (R4 and R6) have received less attention (Table 1), although

these are arguably the two relationships most able to address questions relating to the trophic consequences of dingo control. The direct risks dingoes pose to threatened fauna (R5) should also be well established before positive dingo management can be implemented with confidence [22]. Dingoes are highly adaptable and generalist predators capable of threatening many of the species they have also been predicted to protect [16, 17]. Studies that focus on R2 (and report that dingoes are negatively associated with foxes and cats) typically presume that lethal control of dingoes must therefore benefit foxes and cats (R4), though such an assumption is unfounded [22, 32]. Of ultimate importance however, and irrespective of any of the other relationships, understanding the effect of dingo control on threatened prey species (R6) can facilitate the most rapid management progress. The short-term and direct effects of dingo control on threatened fauna were reviewed in [79], which concluded that no studies to date have shown negative effects of dingo control on non-target fauna, a view subsequently ratified in [84]. There remains, however, limited reliable data on the longer term and indirect effects of dingo control faunal biodiversity [41, 85].

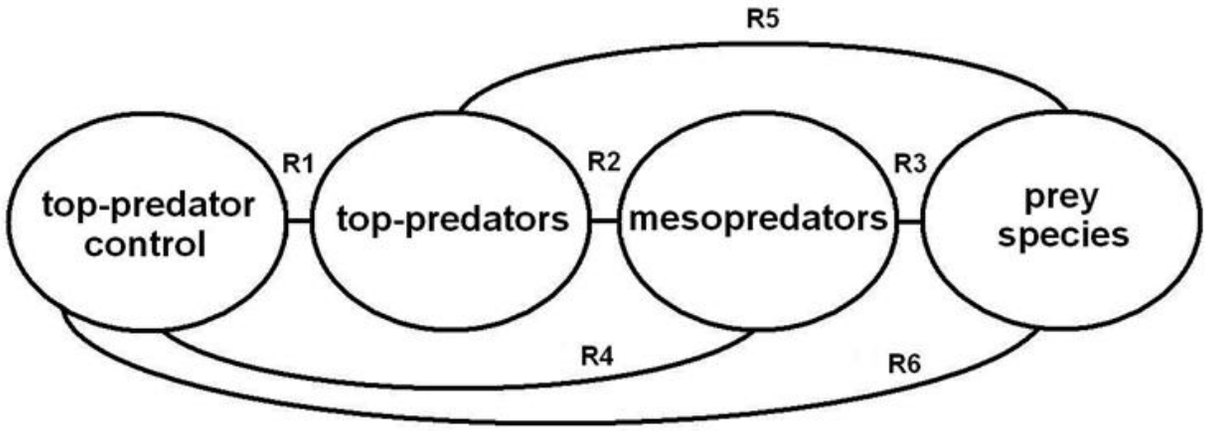

Figure 1. Schematic representation of six relationships (R1–R6) between top-predator control and prey species at lower trophic levels.

Investigating R6 is a 'black box' approach to applied research [86], meaning the observed outcomes of control interventions can enable management progress in the absence of a complete understanding of the mechanisms responsible for the outcomes. For example, [86] summarised the results of 25 years of experimental research on the conservation of threatened black-footed rock-wallabies *Petrogale lateralis*, stating that researchers had found time and again that fox control resulted in more rock-wallabies, but they did not have a good grasp on the mechanisms responsible for it. Thus, if investigations of R6 show that threatened prey populations fluctuate independently of dingo control, lethal control of dingoes might continue to occur without concern from conservationists that such practices inhibit the recovery of threatened fauna through trophic effects. Lethal dingo control may not be incompatible with biodiversity conservation or restoration [32], nor is cattle production always incompatible with dingoes in the absence of dingo control [38, 87, 88]. In a world where resources to manage threatened species are limited, focussing on such applied studies should be of utmost value to land managers and policy makers.

Plate 1. Rufous hare-wallabies *Lagorchestes hirsutus* (bottom right; photo from www.arkive.org), dusky hopping-mice *Notomys fuscus* (bottom left; photo by Reece Pedler) and red foxes *Vulpes vulpes* (top right; photo by Ben Allen) are some of the fauna that are affected both positively and negatively by dingoes (top left; photo by Ben Allen).

3. The state of current evidence for dingoes' ecological roles

Classical manipulative experiments are the best way to advance scientific knowledge [89, 90]. However, performing robust experiments on dingoes at large-enough scales is costly and logistically very difficult or even impossible [41]. Almost all field studies typically sample dingo populations using passive tracking indices (or sand plots) placed along dirt roads and trails. The use of other monitoring techniques, such as camera trapping, are increasingly being used [91, 92]. Although many studies investigating R2 and R5 using passive tracking indices have claimed to provide evidence that dingoes stabilise ecological processes through their top-down effects on sympatric predators and prey, three unresolved issues continue to compromise the reliability of these conclusions for most studies (Table 1):

1. Much of the literature is weakened by methodological flaws (such as seasonal or habitat confounding, or invalid and violated assumptions) which render the reliability of the body of data collected uncertain [52]. In many cases, it is not the technique that is weak, but it is the poor application of otherwise robust techniques that compromise the data collected [51]. This is not to say that the conclusions of such studies are incorrect, but that the reader cannot tell whether they are or not because of the flaws.

2. Regardless of their methodological flaws, most studies are also conducted over small spatial and/or temporal scales. Because of spatiotemporal variation in animal densities [67, 93, 94], behavioural avoidance of top-predators by mesopredators [3, 95, 96], and because most studies sample dingoes along roads (which are favoured by dingoes; [95]), the results of many recent studies may simply be artefacts of sampling biases towards apparent inverse relationships between dingoes and mesopredators.
3. Regardless of methodological flaws or sampling bias, the experimental designs of many studies are still only observational or correlative ([41]), rendering their conclusions subject to a wide variety of plausible alternative explanations [53, 68]. Such studies can only support statements such as 'dingoes *might* perform this role' instead of statements such as 'dingoes *do* perform this role', which can only be made reliably from studies with greater inferential capacity [89].

3.1. Methodological flaws

Critical review has shown that the data in 75% (15 of 20) of recent studies that sampled dingoes using sand plots on roads are potentially confounded by a variety of factors, including (but not limited to) invalid seasonal and habitat comparisons [52]. Dingo activity on roads varies between seasons independent of their actual abundance [52, 97], which can lead to confounding and weakened inferences if not accounted for by the study design. For example, valid comparisons cannot be made between one site sampled in winter and another site sampled in summer, because observed activity differences are likely to be attributable to behavioural changes and not abundance changes. This issue may most easily be understood for reptiles, which usually reduce their activity in winter [98]. For dingoes and foxes, food availability and breeding may drive this variability [19, 99].

Comparisons between different habitats may also be confounded due to varying detection probabilities associated with different habitat types [68, 93]. For example, even if abundance is equal across habitats, animals occupying landscapes with more difficult terrain may utilise roads (i.e. where sampling occurs) more frequently than animals occupying areas which allow more ubiquitous movements (e.g. [100]), with observed activity differences again potentially attributable to behavioural changes and not abundance changes. Moreover, different habitats often have different faunal assemblages, geological and ecological processes (e.g. [101]), which may influence the way some species interact with sand plots placed on roads. Pooling across seasons or habitats may mask differences that could be more easily viewed if separated (e.g. [32]). A variety of assumptions (such as 'footprints of the same species <500m apart and heading in the same direction belong to the same individual' or 'old-looking footprints are *x* days old') are also commonly made (Table 1) and undoubtedly violated ([52]; but see [88, 102-104] for examples). Violation of such assumptions may underestimate dingo distribution or abundance.

Although a wide variety of methodological flaws are evident (Table 1), violation of assumptions and seasonal or habitat confounding may be more important than other flaws, in that they could have greater ecological significance than other methodological errors [52,

93]. Of the 34 studies considered in Table 1, 14 (41%) and 15 (44%) and are potentially weakened by habitat and seasonal confounding, while 12 (35%) made unnecessary assumptions, indicating that multiple studies contain multiple methodological weaknesses. Fundamentally, indices are only useful when they are correlative of abundance [67, 105], and such flaws typically mean that the relationship between observed indices and actual abundances is unknowable. We note however, that accurate knowledge of absolute abundance is near impossible to acquire in the field [67, 105, 106], and we are not aware of any studies of dingoes that have calibrated sand plot activity data with absolute abundance values (because absolute abundance values have not been attainable). However, where the principles outlined in [93, 106] are strictly applied, researchers can acquire reliable estimates of relative abundance, the metric that underpins the vast majority of available field data on dingoes (Table 1).

The use of inappropriate techniques or poor application of otherwise robust techniques reduces the extent to which such data can be used to make reliable statements about ecological processes, and because many studies have made such flaws (Table 1; [52]), much of the available sand plot data on dingoes might be considered unreliable. Overturning this conclusion for any given study requires demonstration that either (1) the methodological flaws described were not made and/or (2) that if made, they did not constitute unreliability [53]. Once collected, it is also rarely possible to un-confound the data using statistical procedures (such as generalised linear modelling) without making the most tenuous of assumptions [52, 105]. The design flaws outlined here are discussed in more detail in [33, 52]. Others [53, 54] have questioned the importance of these flaws, but such methodological flaws are not the only issue undermining evidence for dingoes' ecological roles.

3.2. Sampling bias

An index is a measurement related to the actual variable in question [67, 105, 107] and specific to the circumstances under which the data were collected [93]. Importantly, animal populations are not usually distributed uniformly across the landscape but are instead clumped, producing areas of higher and lower abundance (e.g. [108]). Thus, studies conducted over small spatial scales may acquire severely biased results. For example, the areas sampled in [109] or [110] were very small (<10km2), which likely represented only a fraction of a dingo's home range in such systems [111, 112]. The observed relationships between species within such small areas may have limited applicability outside the areas sampled, where animal abundances may be markedly different (e.g. [108]). Animal activity is also rarely distributed uniformly over temporal scales. Within a 24 hour period, animals may exhibit diurnal, nocturnal or crepuscular behavioural cycles which prevent reliable comparisons of index values from one time period to another. This may be most easily understood for birds, where, for example, observations collected from one area in the early morning should not be compared to observations collected from another area at noon [113, 114]. Many of these considerations essentially amount to issues of detection probability, and have been discussed in greater detail elsewhere [68, 93, 114, 115]. The same principles apply to indexing and population estimation using almost any technique [93, 116].

The highest activity periods for top-predators are also usually optimal, mesopredators usually avoid top-predators during these times, and prey activity usually fluctuates independently of predator activity (e.g. [117-119]). Because mesopredators typically seek to avoid encountering top-predators, mesopredator activity is likely to be lower at times and in places with higher top-predator activity. This has important implications for studies conducted over restricted temporal scales, such as snap-shot or single sample studies (Table 1; e.g. [120-122]). If dingo activity is high on those days, mesopredator activity would be expectedly lower (and vice versa), which means that such temporally limited data is silent on the ability of dingoes to suppress or exclude mesopredator abundances over time, because mesopredators may simply have been avoiding the sampling area on those days. Repeating this snap-shot approach to sampling at any number of multiple sites cannot overcome this issue of bias. Conducting successive surveys over slightly longer timeframes (e.g. three or four surveys over one year) may also be affected by this bias because periods of high or low top-predator activity may endure for several months [52, 97, 111, 123]. Some such studies (e.g. [110, 124]) might been viewed as positive population responses of mesopredators to single dingo control events. Again, however, such observations would be expected given that mesopredator behaviour may change, increasing their use of tracks once the landscape of fear has been altered [96, 125, 126] without necessarily altering their actual abundance (e.g. [110, 124, 127]). Temporally restricted data cannot be reliably used as evidence that dingo control increases the abundance of mesopredators unless the results can be adjusted for seasonal effects by incorporating data from a comparable nil-treatment area. Even over several years, a sampling strategy which focuses on landscape features where dingoes are expected to be more active (such as dirt roads and trails) are also likely to be biased towards dingoes and less sensitive (but not insensitive; e.g. [87]) at detecting foxes or cats [95].

Such issues of bias on sand plots are typically overcome by sampling populations over larger spatial and/or temporal timeframes [93] and means that interspecific comparisons of index values are inappropriate [93, 94]. Other population sampling and analytical techniques might be used (such as estimates derived using photo-mark-recapture [128-131], camera trap rates [132], aerial surveys [133, 134], distance sampling of actual observations or signs [113], occupancy modelling [68] or track transects [135]), but these are all likewise subject to similar issues [114, 116]. Even though magnitudes of index values are meaningless for comparison between species, the population trends defined by the index values over time can be valid given appropriate study design and data analyses [93]. All studies identified in Table 1 have sampled predators for only a few days at a time during each survey, meaning that the results from each individual survey, in isolation, might be artefacts of such bias. This is an important weakness of short-term studies, but when surveys are repeated over several seasons or years, resulting trends may be reliably used to identify relationships between predators. For example, fox activity on sand plots may be much lower than those of dingoes for any (or every) given survey (possibly as a result of sampling bias), but when surveyed repeatedly over longer timeframes, correlations between dingo and fox population trends can be confidently compared. When dingo abundance is further manipulated in an experimental framework, a divergence of activity (or relative abundance)

trends between dingoes and foxes would be particularly strong evidence for mesopredator suppression or release. The corollary of this is that non-divergence of dingo and fox population trends over time would be particularly strong evidence that mesopredator suppression by dingoes is not occurring.

Additional to the methodological flaws described earlier, many studies are also conducted over small spatial or temporal scales (Table 1). Thus, their results are likely to be affected by the sampling biases described, giving the potentially mistaken impression of inverse relationships between dingoes and mesopredators. The common presence of this issue throughout the literature further weakens the reliability of data on dingoes' ecological roles. Such biased data might only be suggestive of spatial avoidance between predators, but it cannot demonstrate avoidance. Provided the proper indexing principles are strictly applied and the data analysed appropriately, studies assessing predator population trends over longer timeframes will have a much better ability to identify correlative relationships. However, to identify causal process for observed correlations still requires experimental designs with even greater inferential ability [89, 90].

3.3. Experimental design

Poor application of methods and sampling bias are but two forms of experimental design flaws weakening the reliability of many studies. But even if such issues are overcome through appropriate sampling strategies, different types of experimental designs have inherent limitations to their inferential ability [89]. The implications of these limitations have not been adequately dealt with in most appraisals of the literature on dingoes' ecological roles. In 2007, [41] concluded that the available data on dingoes' ecological roles was mostly observational and correlative, and many studies published since then (e.g. [31, 78, 122, 136-138]) have not improved this situation. It should be understood that 'studies of a more observational nature can make only weak inferences about cause and effect and studies that involve classical experiments can make stronger inferences. Where studies use more observational methods the results should be interpreted and valued as such, and not as equivalent to the results of classical experiments' ([89]; but see also [90]). The replication and randomisation of treatments, along with the use of nil-treatments (or experimental controls) are particularly important design features that can provide a greater ability to demonstrate causal processes – provided methodological flaws and sampling bias are also avoided.

The inferential capabilities of different designs used in 34 studies of dingoes are here ranked between 1 and 16 (1 = highest level of inference, 16 = lowest; from [89]) in Table 1. Without a nil-treatment, the highest rank a study can achieve is a pseudo-experiment type I (Rank 9). Without randomisation, the highest rank possible is a quasi-experiment type I (Rank 5). For studies comparing the effect of contemporary or historical dingo control practices on predators or prey, many researchers cannot randomise their treatments and are constrained to use areas where dingo control is (or is not) already being undertaken (e.g. [83, 139]). In the case of cross-fence comparisons (e.g. [78, 122, 140]), the results of such non-randomised studies may be subject to plausible alternative explanations that cannot be controlled for [15,

101, 121]. Where possible, treatment randomisation offers one way of addressing these constraints, but has only been undertaken by three studies (Table 1). Only one study [32] has involved a classical experiment on dingoes, where treatments and nil-treatments were also replicated (two of each at one site). Thus, almost all of the available literature reports results from experimental designs which cannot reliably demonstrate cause and effect. Each of these three issues (methodological flaws, sampling bias and experimental design limitations) mean that the evidence for dingoes' ecological roles is not as strong as might be supposed, and each of these issues must be overcome in order to change this view.

As an example of how these issues combine to effect the reliability of data, [121] used footprint counts on dirt roads to derive activity indices for dingoes, foxes and cats at three sites on either side of the dingo barrier fence, which was erected in the early 20th century to exclude dingoes from sheep production lands in south-eastern Australia [141-143]). At two sites, fox activity was reportedly ~2–3 times higher in places where dingoes were rare. At a third site, foxes were only detected where dingoes were rare, and cats were reportedly present in equally low abundance on both sides of the fence [121, 138]. The methodological flaws described earlier (and in [52]) mean that the results of [121] could only be considered 'coarse measures'. Although, [53] argued that coarse measures are sufficient in places where the effect sizes are too large to be explained by the methodological shortcomings (such as seasonal confounding), meaning that the quantitative data may be unreliable but the qualitative patterns may still be recognisable. Importantly however, predator activity can naturally vary in excess of 400% in a matter of weeks or months (e.g. [32, 83, 144]), which means that the effect sizes must be enormous for comparisons made between different seasons to not be affected by season. Regardless, sampling occurred only once over a few days at each of the three sites described in [121]. Because, in such habitats, mesopredators typically avoid roads and dingoes do not [95], the low incidence of fox tracks in the presence of greater numbers of dingo tracks could simply be an artefact of spatial avoidance of roads by foxes on the days that footprint counts were collected. This result may not necessarily reflect the relative abundance of foxes at all, because foxes may have been more active in other parts of the landscape on those days – the infrequent detection of mesopredator tracks would be expected at a time of high top-predator activity (or vice versa). Whether the methodological flaws or the potential for sampling bias are considered important or not, [121] was still only a non-randomised correlative quasi-experiment type I [89], with an inferential rank of 5 out of 16 (Table 1). Hence, the observations may equally be explained by alternative factors, such as the cumulative impacts of livestock grazing [15, 121], thus offering only 'inconclusive' support [53] for the functional relationships between the species studied.

We are not trying to argue here that foxes are actually abundant on the same side of the fence as high-density populations of dingoes, or that dingoes are actually abundant on the same side of the fence as high-density populations of foxes. Rather, we seek only to illustrate that the sampling biases inherent to short-term studies prohibit the demonstration of causal relationships. In no way is the preceding discussion on the state of the literature intended to be personally critical of researchers and authors, because achieving robust experiments is

logistically very difficult [41] and randomisation of treatments is often impossible. Rather, we simply aim to show that whether it is methodological flaws or sampling bias or experimental design limitations, most studies cannot provide strong evidence for causal factors associated with dingoes' ecological roles. It is also important to remember that because perfect experimental designs can be executed imperfectly and imperfect designs may be executed perfectly, neither may enable reliable inference. In other words, correlative or mensurative studies that avoid the flaws and biases described may be just as inconclusive as experimental studies that contain them. As [145] cautioned, 'don't even start the project if you cant do it right', because if the basics are not right, such projects may 'only represent wasted resources' [115].

Reference	Study topic (climate)	Methodological strengths	Methodological weaknesses	Spatial scale per site & sampling effort	Relation-ships investigated^	Experimental design (highest rank of inference)*
Allen B.L. [32]	The effect of dingo control on dingoes (arid)	Manipulative experiment BACI design Random allocation of treatments Treatment replication at some sites Time-series data	Baiting intensity varied within treatments between replicates	50 plots over 50km (x2) 6–10 counts at 4 sites over 2–4yrs	R1	Classical experiment (1) & Unreplicated experiment (3)
Allen L.R. [87]	The effect of dingo control on beef cattle (monsoonal tropics and semi-arid)	Manipulative experiment BACI design Random allocation of treatments Time-series data	No replication at individual sites	50 plots over 50km (x2) 7–19 counts at 3 sites over 3–4yrs	R1, R4, R5, R6	Unreplicated experiment (3)
Allen L.R. [83]	The effectiveness of dingo control campaigns (semi-arid)	Replication of treatments Multiple properties surveyed Temporally intensive sampling Time-series data	Non-random allocation of treatments Non-independence between treatments Baiting intensity varied between properties within-treatments	92–133 plots over 92–133km 16–23 counts at 3 sites over 2–3yrs	R1	Quasi-experiment type I (5)
Augusteyn et al. [146]	The effect of dingo control on dingoes and bridled nailtail wallabies	BACI design Manipulative experiment Time-series data Measured demographic responses of prey	One study site only No nil-treatment	53 plots over 53km 20 counts at 1 site over 5yrs	R1, R2, R5, R6	Pseudo-experiment type VII (15)
Brawata & Neeman [140]	Predator distribution around waterpoints in the arid zone (arid)	Spatial replication of treatments Two indices of predators used	Data confounded by habitat and seasonal effects Used binary observations over potentially continuous measures Two experiments in one, but analysed together Sand plot index data untransformed	15 plots over 20km (x2) and 20 scent stations over 20km (x2) 2 counts at 5 sites over 3yrs	R1, R2, R4	Quasi-experiment type I (5)

Reference	Study topic (climate)	Methodological strengths	Methodological weaknesses	Spatial scale per site & sampling effort	Relation-ships investigated^	Experimental design (highest rank of inference)*
Burrows et al. [147]	The effects of dingo control on dingoes, foxes and cats (arid)	BACI design Three indices of predators attempted Time-series data	Non-random allocation of treatments Invalid assumptions when calculating the activity of predators Data confounded by seasonal differences in predator activity Invalid comparisons between species One index technique (cyanide bait uptake) removed individuals from the population	30–60km tracking transects 25 counts at 1 site over 10yrs	R1, R4	Quasi-experiment type III (7)
Catling & Burt [148]	The influence of habitat on small mammals (temperate)	Mensurative study Standardised design	Data confounded by seasonal differences in predator activity Invalid comparisons between habitats Sand plot index data untransformed	20–35 plots over 4–7km 2 counts at 13 sites over 7yrs	R3, R5	Pseudo-experiment type V (13)
Catling et al. [149]	The effects of cane toads on native fauna (monsoonal tropics)	BACI design Three treatments Different indices for some species	Used binary observations over potentially continuous measures Sand plot index data untransformed	25 plots over 5km 4 counts at 1 site over 2yrs	R5	Quasi-experiment type I (5)
Christensen & Burrows [150] (see also [147])	Reintroduction success of native mammals following predator control (arid)	Two measures of predators used	Invalid assumptions when calculating the activity of predators Predators in 'nil-treatment' areas sampled using an index technique (lethal cyanide bait uptake) that removed individuals from the population 'Nil-treatment' area relocated during the course of the study Cyanide sampling technique biased towards dingoes and foxes Only 1 (of 2) treatment was sampled on 7 of the 8 surveys Not all survey results are reported No analyses undertaken	60km tracking transect 8 surveys at 1 site over 4yrs	R1, R2, R3, R4, R5, R6	Quasi-experiment type IV (8)
Claridge et al. [151]	The effect of predator control on activity trends of forest	Mensurative study Spatial replication of treatments and transects Time-series data	Used binary observations over potentially continuous measures Assumed independence between sand plots	75-125 plots over 19-31km 19 counts at 1 site over 9yrs	R1, R4, R6	Quasi-experiment type I (5)

Reference	Study topic (climate)	Methodological strengths	Methodological weaknesses	Spatial scale per site & sampling effort	Relation-ships investigated^	Experimental design (highest rank of inference)*
	vertebrates (temperate)					
Corbett [152]	Relationships between dingoes, water buffalo and feral pigs (monsoonal tropics)	BACI design Independent indices of some species Calibrated pig and dingo indices with mark-recapture estimates and total counts Time-series data	Used binary observations over potentially continuous measures	55 plots over 400km 27 counts at 1 site over 7 yrs	R5	Quasi-experiment type I (5)
Edwards et al. [102]	Habitat selection by dingoes and cats (arid)	Mensurative study Standardised design	Invalid assumptions when calculating the activity of predators Data confounded by seasonal and habitat differences in predator activity	25km tracking transects (x4) 9 counts at 1 site over 3yrs	R2	Psuedo-experiment type V (13)
Edwards et al. [153]	The effect of rabbit warren ripping on wildlife (arid)	Spatial replication of treatments	Invalid assumptions when calculating the activity of predators Data confounded by seasonal and habitat differences in predator activity Baiting intensity varied between sites	10km tracking rectangle (x2) 8 counts at 4 sites over 2yrs	R1, R2, R5	Quasi-experiment type I (5)
Edwards et al. [154]	The effect of Rabbit Haemorrhagic Disease on wildlife (arid)	Mensurative study Standardised design	Invalid assumptions when calculating the activity of predators Data confounded by seasonal and habitat differences in predator activity Data influenced by rabbit warren ripping at some sites	10km tracking rectangle (x2 at four sites) 8 counts at 6 sites over 2 yrs	R2, R3, R5, R6	Pseudo-experiment type V (13)
Eldridge et al. [88]	The effect of dingo control on dingoes and wildlife (arid)	Manipulative experiment Two measures of predators used	Invalid assumptions when calculating the activity of predators	10km tracking transects (x6) 7 counts at 3 sites over 3yrs	R1, R4, R6	Unreplicated experiment (3)
Fillios et al. [155]	Relationships between dingoes and kangaroos (arid)	Spatial replication of treatments Independent measures of kangaroos and dingoes	Replication devalued by seasonally staggered indexing Data confounded by seasonal and habitat differences in predator activity	25 plots over 25km (x2) 1 count at 6 sites over 1yr	R5	Quasi-experiment type I (5)

Reference	Study topic (climate)	Methodological strengths	Methodological weaknesses	Spatial scale per site & sampling effort	Relation-ships investigated^	Experimental design (highest rank of inference)*
			Sand plot index data untransformed			
Fleming et al [139] (see also [156])	The effects of dingo control on dingoes (temperate)	BACI design Index data transformed Data corrected for detection probability	Non-random allocation of treatments Abundance and activity potentially confounded	120–270 plots over 12–27km (x2) 12 counts at 1 site over 3yrs	R1	Quasi-experiment type 1 (5)
Johnson & VanDerWal [136] (using data from [157, 158])	Dingoes ability to limit fox abundance (temperate)	Source data from mensurative studies Large data set over wide spatial distribution	Source data confounded by seasonal and habitat differences in predator activity Source data used binary observations over potentially continuous measures Invalid comparisons between species Sand plot index data untransformed	From [158]: 45 plots over 18km, 65 plots over 26km and 105 plots over 84km Repeated counts at 3 sites for up to 9yrs From [157]: 20–35 plots over 4–7km 1 or 2 counts at 15 sites over 7yrs	R2	Pseudo-experiment type V (13)
Kennedy et al. [159]	Relationships between dingo control, dingoes and cats (monsoonal tropics)	Mensurative studies and manipulative experiments Spatial replication of treatments Mensurative study temporally replicated Data transformed Time-series data	Site differences not explicitly identified Temporal trends in predator activity not reported	30–50 plots over 30–50km (x10) 3 counts at 2 sites over 3 years, 2 counts at 2 sites over 2–4 weeks	R1, R2, R4	Pseudo-experiment type I (9) & Quasi-experiment type 1 (5)
Koertner & Watson [160]	The impact of dingo control on quolls (temperate)	Uses two measures of efficacy Replication of treatment (individuals exposed)	Used binary observations over potentially continuous measures Index data untransformed	36 plots over 36km 2 counts at 1 site once	R1, R4	Quasi-experiment type I (5) & Pseudo-experiment type V (13)
Letnic et al. [121] (a subset of [122])	Dingoes' role in protecting dusky hopping-mice from predation by foxes and cats (arid)	Spatial replication of treatments Different measures for hopping-mice and dingoes	Replication devalued through seasonally staggered indexing Insensitive measures of grazing pressure used Data influenced by seasonal and habitat differences in predator activity	25–30 plots over 25–30km (x2) 1 count at 3 sites over 1yr	R3, R5	Quasi-experiment type I (5)

Reference	Study topic (climate)	Methodological strengths	Methodological weaknesses	Spatial scale per site & sampling effort	Relation-ships investigated^	Experimental design (highest rank of inference)*
Letnic et al. [122]	Relationships between dingoes and wildlife (arid)	Spatial replication of treatments Different measures for wildlife and dingoes Effect size measured	Replication devalued through seasonally staggered indexing Data influenced by seasonal and habitat differences in predator activity Used binary observations over potentially continuous measures Insensitive measures of grazing pressure used	25–30 plots over 25–30km (x2) 1 count at 8 sites over 2yrs	R3, R5	Quasi-experiment type I (5)
Lundie-Jenkins et al. [110]	Relationships between hare-wallabies and introduced mammals (arid)	Mensurative study Comprehensive dataset collected	Used binary observations over potentially continuous measures Non-independence between plots No details of dingo control program given Very small spatial scale	Intensive plot coverage within a ~10km^2 area 4 counts at 1 site over 1yr	R1, R2, R3, R4, R5, R6	Simple observations (16)
Moseby et al. [109]	Population dynamics of hopping-mice (arid)	Mensurative study Time-series data	Used binary observations over potentially continuous measures Very small spatial scale	4km transect inside an 8ha grid (x2) 15 counts at 2 sites over 8yrs	R3, R5	Quasi-experiment type II (6) or Pseudo-experiment type VI (14)
Newsome et al. [101]	Fence effect on dingoes and wildlife (arid)	Different measures for wildlife and dingoes	Invalid comparisons between species	Ringed plots around 10 waterpoints (x2) 4 counts at 1 site over 1yr	R3, R5	Quasi-experiment type 1 (5)
Pascoe [161]	Predator ecology and interactions (temperate)	Mensurative study Two measures of dingoes used Spatial replication	Used binary observations over potentially continuous measures for some analyses Sand plot index data untransformed	31 plots over 15km 8 counts at 3 sites over 2yrs	R2, R3, R5	Pseudo-experiment type V (13)
Pavey et al. [162]	Population dynamics of rodents and predators (arid)	Mensurative study Different measures for wildlife and dingoes Two measures of dingo abundance collected	Invalid assumptions when calculating the activity of predators Invalid comparisons between species Merged sandplot and spotlighting data	10km tracking transects (x3) 6 counts at 1 site over 2yrs	R3, R5	Pseudo-experiment type V (13)
Pettigrew [124]	The effect of dingo control on cats (arid)	Demographic data on cats collected Two measures of predators used	Ambiguous description of site and methodology Data from both sampling measures apparently combined Data from some treatments not reported	Spatial scale unknown, but ~100km of transect 12 counts at 1 site over 3yrs	R3, R4, R5	Quasi-experiment type IV (8)

Reference	Study topic (climate)	Methodological strengths	Methodological weaknesses	Spatial scale per site & sampling effort	Relation-ships investigated^	Experimental design (highest rank of inference)*
Purcell [123]	Dingo purity, diet, activity and behaviour (temperate)	Mensurative study Temporally intensive sampling	Used binary observations over potentially continuous measures for some analyses Sand plot index data untransformed	25 plots over 25km (x2) 26 counts at 1 site over 2yrs	R2, R3, R5	Pseudo-experiment type V (13)
Southgate et al. [103, 104]	Bilby and predator distribution and fire (arid)	Three different sampling strategies used Different measures of bilbies and predators	Data influenced by seasonal and habitat differences in predator activity Used binary observations over potentially continuous measures Invalid assumptions when calculating the activity of predators Footprints assumed 'old' were excluded from occupancy analysis	10km rectangle tracking transects (x2) 6–8 counts at 8 sites over 4yrs	R3, R5	Quasi-experiment type I (5)
Wallach & O'Neill [120] (a subset of [31, 78])	Relationship between dingoes and kowaris (arid)	Two measures of dingo abundance collected	Data influenced by seasonal and habitat differences in predator activity Invalid assumptions when calculating the relative abundance, "Index of abundance", and territorial activity of predators Data influenced by the presence of pet dogs and people Multiplication of binary and continuous abundance measures Sand plot index data untransformed Small spatial scale	10–12 strip plots (500m long), and 20 area plots (2ha) 1 count at 2 sites once	R2, R5	Quasi-experiment type IV (8)
Wallach et al. [163] (a subset of [31, 78])	Dingoes' role in protecting yellow-footed rock wallabies and malleefowl from predation by foxes and cats (arid, semi-arid)	Two measures of dingo abundance collected Large data set over wide spatial distribution	Data influenced by seasonal and habitat differences in predator activity Invalid assumptions when calculating the relative abundance, "Index of abundance", and territorial activity of predators Data influenced by the presence of pet dogs and people Multiplication of binary and continuous abundance measures Sand plot index data untransformed	9–25 strip plots (500m long), and 21–39 area plots (2ha) 1–2 counts at 7 sites over 1yr	R2, R5	Quasi-experiment type III (7)

Reference	Study topic (climate)	Methodological strengths	Methodological weaknesses	Spatial scale per site & sampling effort	Relation-ships investigated^	Experimental design (highest rank of inference)*
			Small spatial scale			
Wallach et al. [31]	The effect of dingo control on pack structure and social stability (arid)	Two measures of dingo abundance Large data set over wide spatial distribution	Data influenced by seasonal and habitat differences in predator activity Invalid assumptions when calculating the relative abundance, "Index of abundance", and territorial activity of predators Data influenced by the presence of pet dogs and people Multiplication of binary and continuous abundance measures Sand plot index data untransformed Small spatial scale	9–25 strip plots (500m long), and 21–39 area plots (2ha) 1–3 counts at 7 sites over 3yrs	R1	Quasi-experiment type III (7)
Wallach et al. [78]	The effect of dingo control on invasive species (arid)	Two measures of dingo abundance Large data set over wide spatial distribution	Data influenced by seasonal and habitat differences in predator activity Invalid assumptions when calculating the relative abundance, "Index of abundance", and territorial activity of predators Data influenced by the presence of pet dogs and people Multiplication of binary and continuous abundance measures Sand plot index data untransformed Small spatial scale	10–12 strip plots (500m long), and 20–40 area plots (2ha) 1–3 counts at 7 sites over 3yrs	R1, R4	Quasi-experiment type III (7)

Table 1. Methodological details of sand plot studies investigating the relationships between dingoes and faunal biodiversity. ^See Figure 1 for explanation of primary relationships. *See Table 1.2 in [89] for descriptions of experimental designs and rank of inference (rank 1 = highest possible, 16 = lowest possible). Note: different types of experimental design may be possible for some studies depending on the nature of the question/s being investigated, and the designs/rank identified here represent the highest level of design possible from the data collected.

4. The dingo-suppressive effects of foxes

The inability of correlations to describe causation was discussed by [68], and is illustrated here by examining published data on relationships between dingoes and foxes. Intraguild killing and interference competition are the two primary mechanisms given to facilitate the

dominance of one predator over another ([1, 2], and references of studies therein). With some noteworthy exceptions (e.g. [144]), observations of intraguild killing are rare, and its occurrence is most often inferred from the remains of one predator in the diet of another (e.g. [164, 165]). Interference competition is typically inferred from studies of dietary overlap between sympatric predators (e.g. [118, 162, 166]), with high levels of dietary overlap used to infer a high level of potential competition. A variety of such studies have been conducted in Australia, which provide compelling correlative evidence that foxes may suppress dingoes through both mechanisms.

Dingo remains have been found in fox scats (e.g. [123, 164, 167, 168]), and even in cat scats (e.g. [169]), suggesting that these mesopredators kill (or at least consume) dingoes on some occasions. Being 2–3 times larger than foxes, dingoes will likely be victors in aggressive encounters between adults of the two species. However, foxes may be a threat to dingo pups, and dingoes may exhibit heightened activity levels during times when their pups are vulnerable [144]. By limiting recruitment of juveniles, foxes have been observed to suppress populations of one of Australia's largest native herbivores, eastern grey kangaroos M. giganteus [170]. Thus, differences in adult body sizes should not automatically discount the potential for foxes to suppress dingoes also. That mesopredators can slow down recruitment of top-predators was precisely the reason why smaller spotted hyaenas Crocuta crocuta were reintroduced with lions Panthera leo in southern Africa [171]. Multiple studies (e.g. [122, 164, 172, 173]) have also shown foxes to have a high level of dietary overlap with dingoes (Fig. 2), or in other words, dingoes and foxes eat the same things. This suggests that interference competition from high-density populations of foxes (which can reportedly be 7–20 times higher than dingoes [101]) reduces the availability of prey that otherwise might be consumed by dingoes; top-predators being primarily limited by bottom-up factors related to their preferred prey [174-176].

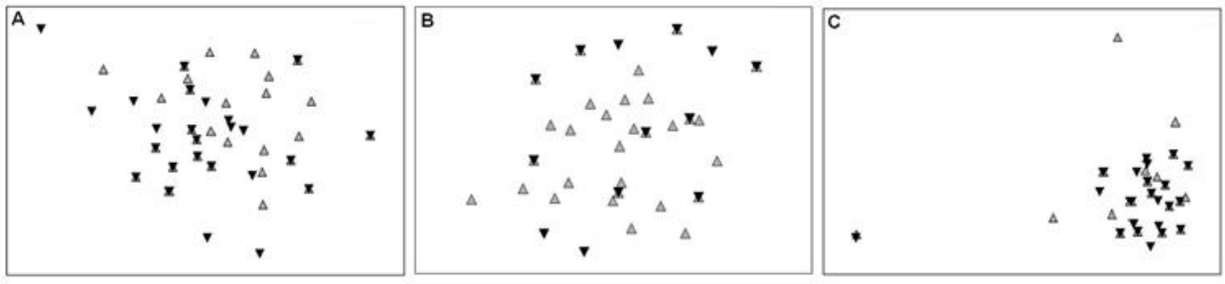

Figure 2. Ordination plot of nonmetric multidimensional scaling analyses showing a high level of dietary overlap between foxes (▼) and dingoes (▲) in the (A) Simpson Desert, (B) Strzelecki Desert and (C) Nullarbor region of arid Australia (from [164]).

Using data from [177], [178] report that dingoes were infrequently detected in places with high fox numbers (Fig. 3). This is further supported by the analyses of [136], which also report that dingo abundance is lower when fox abundance is high (Fig. 4). In contrast, scat indices (or scat collection rates) between dingoes and foxes appeared positively correlated in [123] and foxes (and especially goannas *Varanus varius*) were thought to derive some benefit

from dingoes through kleptoparasitism in [173]. Although there are important limitations associated with the use of scats for making inferences about predation and abundance [16, 17, 61, 179], it appears clear from the data published in the aforementioned studies that a substantial and compelling amount of correlative evidence exists to support the hypothesis that foxes suppress dingoes through direct killing and interference competition. In all cases however, alternative hypotheses have been raised. These include the suppression of foxes by dingoes (e.g. [136, 164]) or the cumulative effect of livestock grazing (e.g. [15, 121]). That multiple plausible and competing alternative explanations can be generated is precisely the reason why correlative evidence cannot be trusted to describe causal processes [68] and most of the presently available literature on dingoes' ecological roles is at best inconclusive [52, 53].

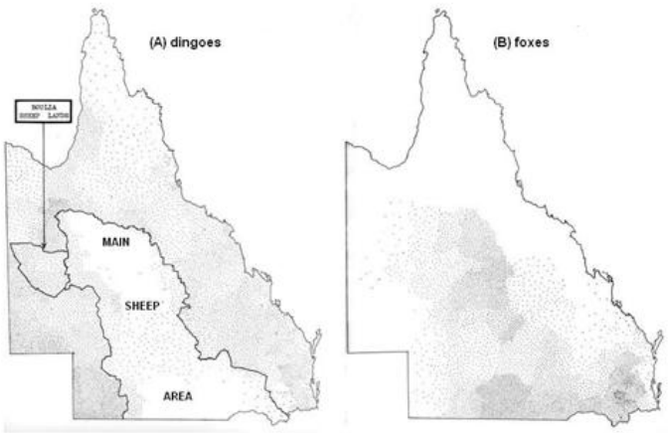

Figure 3. Bounty returns for (A) dingoes and (B) foxes in Queensland for the 1951–52 financial year (from [177], but see also [178]) showing that dingoes were rarely found in the presence of foxes.

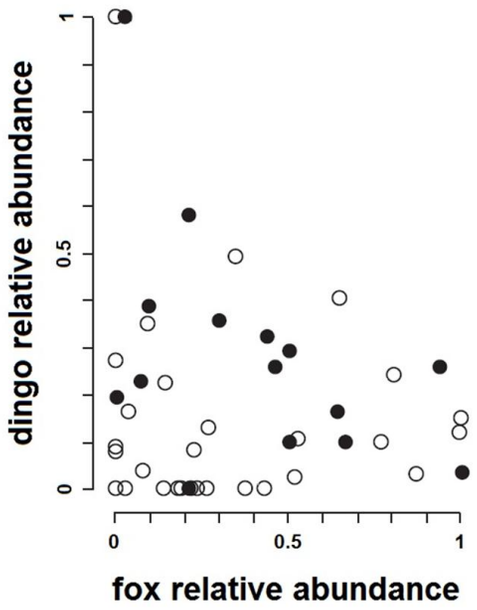

Figure 4. The relationship between dingo and fox abundance in eastern Australian forests (adapted from [136]) showing that the variability in dingo abundance is lower in areas with higher fox abundance (filled circles source data from [101], open circles source data from [157]).

5. What direct risk do dingoes pose to faunal biodiversity?

That dingoes provide net benefits to biodiversity has been almost universally accepted (e.g. [9, 30, 47, 49, 62]) despite the unreliable and inconclusive state of the literature described earlier. Additionally, and disregarded by most, is that dingoes have been implicated in the extinctions of native vertebrates prior to European settlement [23, 180, 181] and the loss of other native vertebrates in the recent past (e.g. [15, 19, 182-185]). Predation by dingoes and other wild-living dogs is therefore identified as a known or potential threat in no less than 14 national threatened species recovery plans listed by the Australian government [17] for species weighing as little as 70 g (i.e. marsupial moles, *Notorycetes* spp. [186]). 'Predation and hybridisation by feral dogs (*Canis lupus familiaris*)' is also a listed Key Threatening Process for 'threatened species, populations, and communities' in New South Wales (see [187] for the listing, see [188] and [57] for the distribution of *Canis* sub-species in Australia, and see [33, 189], [19], [56], [190], [22] for discussion of taxonomy and functional similarities between wild-living sub-species of *Canis*). Dingoes also threaten northern hairy-nosed wombats (*Lasiorhinus krefftii* [184, 191]), bridled nailtail wallabies (*Onychogalea fraenata* [146, 192]) and a range of other species [16, 112, 193, 194] in other areas, where it is predicted that some populations (such as those of koalas *Phascolarctos cinereus* [195, 196], for example) will only persist through the control or absence of canid predators, including dingoes. Not only are many mammals susceptible to exploitation by dingoes, but some bird (e.g. [19, 59, 197]) and reptile (e.g. [112, 198-200]) populations may also be substantially impacted by them. Predation on these less-preferred taxa may increase if mammals become increasingly unavailable [16]. Urgent research focussing on R5 is therefore paramount before positive dingo management is widely adopted in the hope that it will solve our biodiversity conservation problems [16, 17].

Although dingoes and threatened native fauna coexisted sympatrically prior to European settlement, they did not do so in the presence of rabbits, livestock or other landscape-changing effects of pastoralism [23, 70, 201]. Unequivocal data on dingo densities may not have been collected at the time, but post-European provision of virtually unlimited prey and water resources across much of Australia has undoubtedly increased the range and population densities of dingoes in areas outside the dingo barrier fence [19, 112, 202]. Thus, populations of many native fauna have not been exposed to such high and ubiquitous densities of dingoes until modern times. Put simply, the circumstances have changed significantly since dingoes and now-threatened native fauna coexisted sustainably [15, 22], where habitat alteration now enables dingoes (and other predators) to exploit populations that otherwise might have sustained dingo predation. Thus, dingoes clearly present direct risks to threatened fauna that must not be casually overlooked or assumed to be of lesser importance than their indirect benefits [16, 17, 22]. For example, by applying established predation risk assessment methods [50] developed for foxes and cats, [16] showed that up to 94% of extant threatened mammals, birds and reptiles in western New South Wales would be at risk of dingo predation (71% at high risk) should dingoes re-establish there (Table 2). By comparison, only 66% and 81% were predicted to be at risk of cat and fox predation [50].

	Low dingo density			High dingo density		
	No risk	Low risk	High risk	No risk	Low risk	High risk
			EXTANT MAMMALS (n = 16)			
Vulnerable	4	2	2	0	2	6
Endangered	1	5	2	0	0	8
TOTAL	**5**	**7**	**4**	**0**	**2**	**14**
			EXTANT BIRDS (n = 41)			
Vulnerable	16	13	2	4	12	15
Endangered	1	5	4	0	1	9
TOTAL	**17**	**18**	**6**	**4**	**13**	**24**
			REPTILES (n = 23)			
Vulnerable	3	5	4	1	1	10
Endangered	2	5	4	0	2	9
TOTAL	**5**	**10**	**8**	**1**	**3**	**19**
			LOCALLY EXTINCT MAMMALS (n = 17)			
TOTAL	**2**	**6**	**9**	**2**	**0**	**15**
			LOCALLY EXTINCT BIRDS (n = 4)			
TOTAL	**2**	**1**	**1**	**0**	**2**	**2**

Table 2. Summary of overall dingo predation risks to 80 threatened extant and 21 locally extinct mammals, reptiles and birds in western New South Wales (from [16]).

Information on prey important to dingoes seems particularly useful for gauging the potential risks dingoes pose to threatened fauna [16]. While the mere presence of threatened species in dingo diets might be dismissed as uncommon events [169, 203, 204], 71% (33 of 47) of dingo diet studies assess <500 scat or stomach samples [17]. Greater sampling effort and a consideration of additional information has highlighted substantial risks to threatened fauna from dingoes in some cases (e.g. [17, 61, 112]). For example, threatened mammals under 35 g body weight are typically considered to fall outside the primary weight range [75, 205] of preferred prey for dingoes [19], but ([112]; N = 1907 scats) showed that anthropogenic provision of virtually unlimited food and water resources can exacerbate the risk of decline for some such species by facilitating elevated levels of dingo predation (i.e. hyperpredation [10, 206]). In another example, ([17]; N = 4087 scats) reported that although small rodents featured relatively infrequently in dingo scats while rabbits or kangaroos were available, consideration of dingo predation rates on rodents (made possible by knowledge of predator and prey densities) supported earlier assertions by [207] that dingoes alone have the capacity to exterminate rodent (e.g. dusky hopping-mice *Notomys fuscus*, Plate 1) populations within a few months under certain conditions, regardless of any

indirect benefit rodents may derive through dingoes' effects on foxes and cats [17]. Even seemingly unsusceptible arboreal and fossorial species (such as sugar gliders *Petaurus breviceps* and beach crabs *Ocypode* spp.) can become important prey for dingoes following the decline of their preferred prey ([61]; $N = 1460$ scats). Using the simple formula:

$$\text{Number of months until population extinction} = \frac{a}{\left(\frac{\left(b \times \left(365 \div 100\right)\right) \times c}{d}\right) \div 12}$$

where a = mean prey density, b = % occurrence of prey in scats, c = mean dingo pack size, and d = mean home range size of a dingo pack, the consideration of predator and prey densities can illuminate the significance of infrequent records of threatened species in dingo diets (Table 3).

Example	Dusky hopping-mice (from [17])	Rufous hare-wallabies (from [110])	Bridled nailtail wallabies (from [146])	Black-footed rock-wallabies (from [182])
Frequency of occurrence in dingo scats (%)	8*	12*	8*	46*
Mean dingo pack size (*N*=)	10*	10#	8^	5#
Mean dingo home range size (km^2)	25*	50#	40^	50#
Prey density (individuals/km^2)	60*	5#	5*	<1*
Predicted number of months until population extinction by dingoes	**3.08**	**6.85**	**10.27**	**0.71**

Table 3. The hypothetical impact of dingo predation on four threatened species based on the frequency of occurrence in dingo scats and predator and prey densities. (See [17] for rationale and assumptions; *Empirical data reported in original studies; ^L. Allen, unpublished data; #estimated values based on comparable studies).

As an example, [110] report the swift extinction of the small and last remaining mainland population (outside of fenced reserves) of rufous hare-wallabies *Lagorchestes hirsutus* (Plate 1) in 1987 when one or two foxes were detected first on only one occasion in an area that had just been exposed to a dingo control program. A cursory view of this outcome might suggest that dingo control facilitated the mesopredator release of foxes and led to the local extinction of a critically endangered species [41], but this does not explain the driver/s of hare-wallaby decline in the first place. Lethal dingo control had not previously occurred in the area until <100 poisoned baits were distributed along 20–30 km of vehicle tracks within the 10 km^2 area surrounding the hare-wallaby population (G. Lundie-Jenkins, unpublished data), so it could not have been lethal dingo control that caused the decline of the hare-wallabies. Foxes were reportedly absent (or at least uncommon [208]) until the dingo control program

occurred [110], so it could not have been foxes which caused the decline either, and cats (which were also in very low abundance [110]) had probably been there for several decades [208, 209]. Notably, artificial water resources had not been established in the area until the 1950s and 1960s when outback mining and pastoralism became established [15, 112]. This undoubtedly increased the density and distribution of dingoes [112, 202] (the primary terrestrial predator of hare-wallabies since the extinction of thylacines [23]), suppressed any extant fox or cat populations, and caused or contributed to the decline of hare-wallabies and other marsupials [15, 19]. Furthermore, hare-wallabies were present in 12% of dingo scats collected prior to the commencement of the study [110]. Hare-wallaby densities were not reported in [110], but considering that the population became extinct just a few months later, there may have been only 50 or so animals (at most) in the population (G. Lundie-Jenkins, pers. comms.). If dingo densities were 0.2/km^2 (or 10 individuals within a home range of 50 km^2) and hare-wallaby densities were 5/km^2 (or 50 individuals within the 10 km^2 study site), and assuming that one scat represents the prey eaten by a dingo in the previous 24 hours, then 12% occurrence in dingo scats could hypothetically represent as many as 438 hare-wallabies consumed by dingoes within the home range of a dingo pack each year. In other words, dingo predation alone had the capacity to exterminate the population of hare-wallabies in <7 months if they could not sustain the loss of that many individuals annually (Table 3). That dingoes were considered to be a limiting factor for their already endangered populations [110] (which is why lethal dingo control was initiated in the first place) suggests that, in association with other causal factors, increased dingo predation over the preceding 30–40 years (a consequence of adding water and dingo prey resources to the area) drove hare-wallabies down to a point where foxes just happened to be the predator to finish the extinction process.

In a somewhat comparable situation, [185] reported that one individual dingo in a dingo-controlled area (which was not detected on sand plots, but from post-mortem evidence on killed animals) was responsible for the surplus killing of 14 (out of 101) reintroduced (and similar sized) burrowing bettongs *Bettongia lesueur* on the first night after release, the rest succumbing to predation by unknown predators within a few months. It should also be noted that the simple calculations described earlier (in Table 3) falsely assume that predation rates remain constant as the prey population declines [17], which limit firm assertions from these considerations. But if the occurrence of a given species in dingo diets is known and a few key assumptions seem reasonable (discussed in [17]), then undertaking this coarse and hypothetical exercise can indicate whether or not dingoes should be considered a potential risk to the population before positive dingo management is implemented. From the preceding discussion, it should be clear that dingoes are certainly not the type of predator that one would want around a population of threatened fauna and should, as a precaution, be considered a significant threat until robust evidence suggests otherwise.

6. Practical issues hampering the realisation of net dingo benefits

Dingo suppression of mesopredators and herbivores are the two primary mechanisms predicted to generate positive biodiversity outcomes for fauna following positive dingo

management (e.g. [23, 78]). Herbivore suppression is expected to increase the food and shelter available to threatened species, mesopredator suppression is expected to decrease predation on the same species, and dingoes are simply the tool expected to generate these outcomes. While the ecological theory supporting these mechanisms might be considered sound (e.g. [4, 6]; but see [210, 211] for an alternative considerations), at least two practical factors may prevent the realisation of these expected benefits in the rangelands of south-eastern Australia (where positive dingo management is considered imperative [50]).

6.1. Livestock enterprise switching

Sheep, goats, kangaroos and rabbits may be considered the most widespread and ecologically important herbivores in this area [34, 101, 212], but in places where two or more of them are extant, using dingoes to disentangle their cumulative impacts may be very difficult to achieve. Assuming that dingoes can suppress agriculturally non-productive herbivores (such as rabbits or kangaroos) without also suppressing the livestock with which they coexist, any reduction in undesirable herbivores may be replaced by increased stocking of agriculturally productive herbivores (such as sheep, goats or cattle), thereby maintaining total grazing pressure. For example, sheep populations have suffered precipitous declines in central and southern Queensland over the last decade [213], with no substantial change in the combined grazing pressure of sheep and cattle because of enterprise switching from sheep to cattle (Fig. 5), which are now in much higher densities in the area. Hence, enhancing the prospects for biodiversity conservation by securing improvements in vegetation communities might only be achievable if livestock stocking rates are not increased following the decline of some herbivores. But such may be a trivial consideration anyway, because dingoes are unlikely to kill only livestock competitors without also killing livestock [37, 189]. Importantly though, the positive management of dingoes may be advantageous to livestock producers where dingoes have greater effects on livestock competitors than they do on livestock ([39]; i.e. in arid cattle production regions), but this may not be economically or socially acceptable in places where the impacts of dingoes on smaller livestock species are prohibitive (i.e. sheep and goat production zones).

It should be understood that dingoes can completely eliminate sheep and goat populations [37, 44, 158, 212], and although their extirpation from rangelands might be considered a biodiversity success to some, the global human population need the food and fibre products these livestock produce [214-217]. As the world's largest wool exporter, the largest goat-meat exporter, and the second largest sheep-meat exporter (www.fao.org; www.mla.com.au), the loss of Australia as a globally important supplier of small ruminant products (which dingoes are quite capable of achieving [15, 61, 142, 218]) would need to be countered by an increase in livestock production in other countries. These countries may not be able to produce them as environmentally or economically sustainably as Australia; they may have extant diseases and other pathogens (such as rabies or screwworm flies *Cochliomyia* spp.) that inhibit broad-scale production or export, be forced to clear new land for increased livestock production, or may also have native predators of their own that need controlling in order to viably scale-up their production of livestock. In short, the primary reason for

encouraging dingoes in sheep production areas (i.e. to improve biodiversity outcomes) may simply shift the biodiversity conservation problem to other countries where, unlike Australia, the extant top-predators may not be very common and their management may be more complex. These, and other issues will need serious consideration before dingoes are permitted to increase in sheep and goat production areas [22, 219].

Figure 5. Trends in sheep (dotted line), cattle (dashed line; assuming 8 DSE per cow) and combined (solid line) livestock numbers in southwest and centralwest Queensland 1990–2010 (Australian Bureau of Statistics data, cat. no. 7121.0, Agricultural Commodities Australia, available at www.abs.gov.au).

6.2. Mesopredator release

Although many threatened fauna are indeed at risk of fox and cat predation [50], these fauna may also be equally at risk of dingo predation [16]. Dingoes do not kill only cats, foxes and kangaroos. In fact, these species are relatively uncommon in dingo diets [17, 19, 220], which means that replacing foxes and cats with dingoes (assuming dingoes could achieve this) or simply adding dingoes to an ecosystem might not stem the decline of threatened species [22]. As strongly interactive species, top-predators can have disproportionate effects on mesopredators, where small increases of larger predators dramatically reduce the abundance of smaller ones [1, 2]. Thus it is hypothetically conceivable that small increases in dingo abundances might substantially suppress foxes, leading to a net reduction in predator biomass and predation on threatened species. This does not appear to have been studied in great detail in Australia (Table 1) but may nevertheless prove true in some cases. Even so, the resulting lower levels of predation on threatened species might still be unsustainably high (which is why knowledge of R2 is of lesser value than R5 when considering the positive management of dingoes). In this situation, higher densities of dingoes might simply force threatened species to extinction slower than higher densities of mesopredators – the end result (extinction) being the same no matter which predator is most common (Table 3). Where multiple generalist predators are capable of exploiting the same prey species (as is the case with dingoes, foxes and cats [162, 164, 165, 172]), attempts to identify which predator is worse may be largely unhelpful in securing biodiversity against decline [221,

222]. Rather, identifying the population viability or status of threatened fauna under different management scenarios (R6) may be more useful.

A review of 14 cases of mesopredator release (analysed pairwise [223]) showed positive mesopredator population responses to decreases in higher-order predator abundance, suggesting that increases of dingoes might suppress foxes yet increase populations of cats, which are lower-order predators apparently suppressed by foxes [224]. Some support for this is found in several studies. Cats appeared to be positively associated with dingoes in the Tanami Desert of the Northern Territory [208], which is at the edge of foxes' national distribution [34, 99]. At tropical study sites devoid of foxes, [159] also reported that cats were positively associated with dingoes in the Northern Territory. At similar sites in the Kimberleys, [159] reported that (besides one outlier) cat activity varied little (0.18–0.40 tracks/sand plot/night) despite a nearly four-fold difference in dingo activity (0.80–4.30 tracks/sand plot/night). The cross-fence study of [121] (a subset of the data in [122]) also reported that foxes and cats were negatively and positively correlated with dingo presence, respectively, suggesting that increased dingoes may suppress foxes yet release cats from suppression by foxes. Subsequent analyses of the more comprehensive dataset suggested that cats were in equally low abundance on both sides of the fence [122], suggesting that cat abundance operated independently of the type of top-predator (dingoes or foxes) present.

Although increased populations of dingoes may reduce mesopredator activity they are unlikely to extirpate or exclude them (e.g. [118, 144, 225]). Detailed studies in northern South Australia ([225]; B. Allen, unpublished data from [32]) report the persistence of foxes in the presence of extremely high densities of dingoes, [144] reported that even though dingoes killed foxes they could not exclude them, and [118] showed that dingoes are unable to limit the distribution of foxes at landscape scales. Indeed, the colonisation and subsequent widespread distribution of foxes and cats across Australia [34] would suggest that the presence of dingoes (or the absence of lethal dingo control) neither prevented their establishment or limit their distribution. Rather, dingoes might reduce their densities and alter their behaviour at local scales [118], but whether or not this provides any relief to threatened prey remains unclear.

Given that dingoes are unlikely to extirpate cats, that there is strong overlap in the diets of dingoes, foxes and cats, and that cat predation is listed by the Australian Government as a Key Threatening Process to 18 of the 19 threatened arid-zone mammal species [122], there may be little overall biodiversity conservation benefit to species threatened by both foxes and cats if dingo populations increase [16, 22]. Irrespective of this, the positive management of dingoes would be unnecessary for places with extant (and typically unmanaged [32]) dingo populations, such as areas outside the dingo barrier fence, which are (confusingly) the very areas where some predict their positive management to be of most benefit to threatened fauna [122]. As illustrated earlier for rufous hare-wallabies and in addition to a variety of other important factors (discussed in [71, 72, 74, 226]), at-risk fauna are clearly threatened by predation per se, and not dingo *or* fox *or* cat predation individually (e.g. [221, 222, 227]). The literature is replete with examples of reductions of one pest animal increasing the undesirable impacts of another with no (or worse) overall outcomes for the species of

conservation concern (e.g. [12, 110, 228]), and it would be naive to expect the positive management of dingoes across large areas to achieve universally 'good' outcomes for faunal biodiversity at more local scales [16, 22]. Increasing the number of generalist predators may only widen the suite of prey susceptible to predation and subsequent decline [222], and 'one may ask if the faunal biodiversity outcomes are any greater if a species is extinguished by a dingo instead of a fox or feral cat' [22]. Moreover, the biodiversity benefits expected of dingoes are likely to be available only to those prey species which have survived the impacts of cats, foxes and dingoes anyway. Thus, if fox and/or cat impacts are not the limiting factor for threatened species, then encouraging the suppression of foxes and cats by adding dingoes to the ecosystem seems an unlikely prerequisite for their recovery [16].

7. Context-specific management

Dingo impacts, roles and functions are context-specific, and the same is true for other top-predators [5, 229]. For example, the positive effects of wolves on biodiversity in some places may not be as apparent in other places just a few kilometres away, where site-specific factors may affect the strength of influence wolves have in the ecosystem [230, 231]. Such context-specific impacts mean that extreme caution should be exercised when considering using top-predators as biodiversity conservation tools in some new context, based on information collected from another time and place [22, 229]. Bottom-up factors associated with prey availability (such as habitat productivity, structural complexity etc) will affect the density of predators [174-176], the density of prey species [232-234] and their relative vulnerability to predation [221, 222, 227, 235]. Within this diversity, land use also varies from conservation to agriculture, from extensive to intensive livestock enterprises, and from small livestock to cattle production (e.g. [15, 69]). It is, therefore, unreasonable to expect that the goals and outcomes of dingo management will be uniform across Australia, which is why dingoes are presently managed locally for where they are and what they are (or are expected to be) doing [33, 35, 64].

Should positive dingo management to be adopted across large areas, the negative impacts of dingoes expected in some contexts may not be manageable in others. For example, the presence of dingoes has been predicted to benefit some rodents in arid environments [47], but dingo predation alone has the capacity to exterminate local populations of the same rodents under certain conditions (e.g. during droughts; Table 3; [17]) – conditions that are predicted to become more frequent and intense under future climate-change scenarios [236-238]. The negative impacts of dingoes in livestock production areas may also become increasingly unmanageable as dingoes are encouraged in adjacent conservation reserves where their impacts might be positive. Radio and GPS tracking studies indicate that most dingoes are sedentary (e.g. [108, 111, 239, 240]), and a recent continental-scale gene flow study [57] supports this conclusion. But a substantial proportion of dingoes do travel considerable distances (e.g. >550 km in 30 days [97]) for dispersal and exploration (e.g. [97, 123, 239, 241]). Given the capacity for dingoes to disperse, without containment fencing, dingo populations and their impacts (like reintroduced wolves [8]) are unlikely to remain only in reserves.

These issues are outside the capacity of any one individual or agency to manage, and are best addressed through a strategic adaptive management approach that can accommodate differences in situation and objectives [242-244]. The management of dingoes (either positively or negatively) requires adherence to a number of underlying principles including: defining the biological assets to be protected and the people involved, setting measurable goals and timeframes for action, undertaking management actions at a scale appropriate to the enterprise or ecosystem to be enhanced and the wild dog home range and movements, relying on a suite of actions applied in a coordinated sequence, and continuously monitoring in preparation for new incursions or threats [35, 64]. Issues of scale and management unit are particularly important, and the minimum size of the management unit may be determined using the home range size of the animal in the particular environment as a guide. Recorded home range sizes for dingoes vary from 7–2013 km^2 in semi-arid and arid rangeland rangelands, from 2–262 km^2 in mesic environments, and may be <1 km^2 in urban areas [19, 112, 239, 245]. Such variation in scales important to dingoes is likely to preclude management approaches which seek to apply broad-scale solutions to context-dependant problems, such as the widespread prohibition of dingo control for the recovery of an isolated population of threatened mammals.

Although dingo management policies must be general by nature, the process of defining the issue in strategic management ensures that the appropriate scale for actions is decided before commencement. Therefore, where dingoes are determined by reliable experimentation to be important for biodiversity conservation, strategic management can achieve this objective locally or regionally, depending on the minimum size of the management unit required. In short, top-down management approaches which seek to exclude the land manager in favour of government policy intervention (e.g. [70]) and/or apply broad-scale solutions to context-dependant impacts (either positive or negative) are unlikely to succeed in restoring faunal biodiversity [22, 246].

8. Looking forward: surmountable challenges to overcome

Knowing that the available data is lacking rigour and defensible or definite conclusions may seem depressing after the countless hours of hard work expended by many in obtaining it. But all is not lost, and dismissing it completely may be just as dangerous as embracing it uncritically [53]. From the implications of [52], [95] and the present study it seems clear that a greater understanding of the advantages and limitations of sand plot tracking indices are required by many dingo researchers, and it will be difficult in reaching consensus on the state of the available literature until this is achieved. The advantages and limitations of indices and populations estimation procedures have been widely discussed (in [67, 93, 94, 105, 106, 114-116, 247-249]; to cite just a few) to a point where relative abundance indices can be viewed as an incredibly powerful population censusing technique provided appropriate principles and analyses are applied [93, 114]. Moreover, so long as the results of studies with lower inferential ability are valued above those with designs that permit more definitive statements, end-users of the literature may also continue to be confused about the most appropriate dingo and threatened species management strategies. A return to more objective and applied science and management of dingoes is imperative (also suggested by [189]).

Long-term manipulative experiments are able to advance science much more rapidly than other approaches [68, 89, 90], but they are few (Table 1), and more are sorely needed [41, 250]. When conducting such studies, the relationships (Fig. 1) and knowledge gaps being investigated are of utmost importance. Interest in the positive management of dingoes as biodiversity conservation tools is ultimately driven by the desire to improve the status of threatened fauna through trophic effects (e.g. [23, 50]), so should not the threatened faunal response to dingo management be the variable of interest? Demonstration of sustained non-target population responses to predator control can provide 'conclusive proof' [79] for the effects of lethal dingo control on threatened fauna. Hence, in places where dingoes are actively controlled (for whatever reason), it is not the direct or indirect effects of dingoes on fauna that should be of primarily interest, but rather, the effects of dingo management practices on fauna (R6) – the 'black box' approach [86]. Knowledge of the other relationships (R2, R3, R5) is supplementary and may be more important in places where dingoes are typically unmanaged.

In order to focus our collective attention on the questions that matter most, we issue the following challenge. For any given site and population of threatened species:

1. Do contemporary dingo management practices negatively affect the species either directly or indirectly?
2. Do dingoes themselves pose a current or future threat to the species, regardless of their indirect effects on other threatening processes?
3. Is positive dingo management the only practical option to improve conditions for the species?
4. What factors determine which predator becomes ecologically dominant following dingo control programs?

If contemporary dingo management practices (such as poison baiting, trapping or shooting) do not harm threatened species either directly or indirectly (R6), then arguments to cease controlling dingoes remain unjustified on biodiversity conservation grounds. Multiple studies have failed to demonstrate the 'release' of mesopredators following dingo control (R4) (e.g. [87, 88, 159, 251], and no studies to date have shown short-term negative responses from populations of non-target species to dingo or fox control [79]. Hence, lethal dingo control will still be useful in mitigating livestock losses without fear of releasing mesopredators or harming threatened species. If dingoes threaten a particular species to any degree (R5), then researchers must investigate the relative strengths of dingo-prey (R5), mesopredator-prey (R3), and dingo-mesopredator (R2) interactions in order to gauge the likely outcomes of positive dingo management. Positive dingo management is unlikely to benefit the threatened species where the direct effect of dingoes is greater (or may become greater) than their indirect effect on mesopredators.

If dingo control does appear to hinder the conservation of the species, and dingoes do not pose a current or future threat to them, are there any alternative management actions that could improve biodiversity outcomes without compromising livestock production values? For example, livestock guardian dogs might offer a non-lethal approach to reduce the impacts of dingoes on livestock without excluding dingoes from an area [252, 253].

Alternatively, the selective exclusion of agriculturally non-productive herbivores from watering points [254-256] may elicit a greater bottom-up response from threatened species than the top-down suppression of mesopredators by dingoes without threatening the viability of livestock producers. In fact, doing so would probably enhance their viability.

Lastly, the commonly observed presence of foxes in areas free of dingo control suggests that bottom-up factors may largely determine which predator successfully colonises and dominates an area, though these influences remain largely unknown. Foxes appear to be positively associated with disturbed agricultural habitats in a bottom-up manner [257, 258], which may help explain the pattern of fox densities noted by [178] and others (e.g. [50]). Top-predators can also be associated with higher biodiversity in a bottom-up manner [19, 174, 175, 229], and positive correlations between dingoes and greater biodiversity values cannot be immediately interpreted to be the result of top-down processes [52, 68]. When the factors that determine which predator dominates a given area become well understood, our ability to manage predators will be greatly enhanced.

9. Conclusion

Maintaining top-predator function may be an important component of biodiversity conservation initiatives in many places [1, 2]. Although this might be more easily achieved in relatively intact areas, the functions of top-predators may be most needed in the more degraded ecosystems characterised by depleted faunal and floral communities. Importantly though, such systems are typically those used most heavily by humans for agricultural production, and the age-old battle betweens humans and top-predators seems likely to continue into the foreseeable future [214, 259]. Nevertheless, conservative environmental management is required in our efforts to balance the needs of humans with those of the threatened fauna and flora we seek to protect [260]. Evidence-based biodiversity conservation and carefully considered policy approaches are critical to the informed management of top-predators for this purpose [261, 262].

This chapter has discussed the knowledge and management of dingoes for biodiversity conservation. Our overview of the field data underpinning knowledge of dingoes' ecological roles has identified critical knowledge gaps that we believe require the primary attention of researchers and policy makers operating in this area. We have also shown that although dingoes are well-studied, their functional roles may not be well understood. This is because methodological flaws, sampling bias and experimental design limitations inherent to most studies (Table 1; [52]) cannot provide reliable or conclusive evidence for dingoes ecological roles. We therefore agree with [53] that there is inconclusive evidence for the positive roles of dingoes and that cessation of lethal dingo control is presently unjustified on biodiversity conservation grounds. We are cognizant that questioning the conclusions of studies documenting the benefits of fox control on native fauna [263] probably delayed the necessary implementation of broad-scale fox control for biodiversity conservation in many places. Likewise, we acknowledge that questioning the science underpinning the role of dingoes may delay the adoption of positive dingo management in places that might yet be

shown to need it. However, we believe there are sufficient concerns regarding the impacts of dingoes on mesopredators and threatened fauna to stress strong caution when considering the positive management of dingoes for biodiversity conservation purposes under current ecological conditions [22].

We therefore challenge researchers and funding agencies to focus on applied science questions that can address the effects of dingo management practices on prey populations of interest. Doing so within an experimental framework that has the capacity to explore and exclude alternative hypotheses will be most useful, and we encourage those with such data to invest time in its analyses and publication. We encourage the continued interest in dingoes as a biodiversity conservation tool, and look forward to the results of future studies on this charismatic and iconic terrestrial top-predator.

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