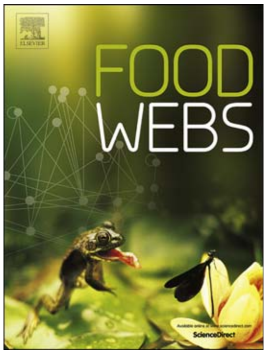

The case for a dingo reintroduction in Australia remains strong: A reply to Morgan et al., 2016

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The case for a dingo reintroduction in Australia remains strong: a reply to Morgan et al. 2016.

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In their paper "Trophic cascades and dingoes in Australia: does the Yellowstone wolf-elk-willow model apply?" Morgan et al. (2016) argue that the case for dingo reintroduction in Australia, based on trophic cascade theory, is "weak". They conclude that, "because of climate instability, the strong top-down trophic responses reported from the Yellowstone National Park case study are unlikely to apply in arid and semi-arid south-eastern Australia and are speculative at best".

We agree that dingoes (*Canis dingo*) are likely to exert different effects on ecological communities in Australia as compared to grey wolves (*Canis lupus*) in North America. A comparison of body sizes and dietary preferences between these canid species alludes to their functional ecological differences. Differences in the biological communities and climate between Yellowstone National Park and Australia also prevent direct comparisons of trophic cascade-processes between the two regions. These facts should not, however, preclude examination of the efficacy and consequences of dingo reintroductions in Australia.

We contend that Morgan et al. (2016): (1) misunderstand the circumstances that make trophic cascades important to consider in Australia, (2) do not acknowledge key reasons why dingo reintroduction has been proposed, (3) haven't recognised the different pathways by which dingoes could influence ecosystems via trophic cascades, and (4) do not fully acknowledge literature and theory relevant to understanding the interplay of bottom-up and top-down processes in Australia. Our reply is intended to assist managers and decision makers when deciding whether or not to reintroduce dingoes into Australian ecosystems.

The circumstances that make trophic cascades important to consider in Australia

Morgan et al. (2016) correctly point out that the interplay between top-down and bottom-up processes is central to trophic cascade theory, but they also posit that “unstable climates are likely to have weak or absent top-down forcing” and that “bottom-up forces likely predominate due to irregular pulses of suitable growing conditions in response to unpredictable rainfall which in south-eastern Australia are exacerbated by nutrient-poor soils”. However, these statements and subsequent trophic models (Figure 1b in Morgan et al. 2016) fall short of recognising that even if top-down trophic interactions in Australia are irregular, they are still critically important. Indeed, dingo-induced suppression of mesopredators such as the red fox (*Vulpes vulpes*) and feral cat (*Felis catus*) appears to be strongest during prolonged periods of low rather than high productivity (Greenville et al., 2014). These periods of low productivity are most crucial for the persistence of small prey species (e.g. small mammals) because they represent times when these prey species are most vulnerable to predation pressure by mesopredators. Predation rates on large prey, including red kangaroos (*Osphranter rufus*) (based on dietary intake), have also been shown to be greatest during periods of low productivity (Corbett and Newsome, 1987). Moreover, prolonged periods of low productivity are the norm in arid Australia, with periods of high productivity only occurring at infrequent and brief intervals associated with extreme rainfall events (Letnic and Dickman, 2006). Therefore, the circumstances under which dingoes can provide net positive effects on ecosystems via trophic cascades (see Letnic et al. 2009) are those that typically prevail.

Why dingo reintroduction has been proposed

Throughout their paper, Morgan et al. (2016) refer frequently to a paper that outlines how dingo reintroduction could be carried out in arid or semi-arid regions of Australia. They state that the proposal by Newsome et al. (2015) is based “on the notion of a canid-driven trophic cascade as per the Yellowstone model” and that the plan assumes “a similar ability of Northern and Southern Hemisphere top-order predators to influence ecosystem structure...”. However, a key premise of the proposal by Newsome et al. (2015) is that, if a dingo reintroduction was undertaken under an experimental framework, it would allow for a comprehensive assessment of the ways in which dingoes can affect ecosystems via trophic cascades. In doing so, the proposal answers the call to undertake manipulative experiments to further examine the ecological role of the dingo (see Allen et al., 2013; Fleming et al., 2012; Hayward and Marlow, 2014). Newsome et al. (2015) mention grey wolf reintroduction into Yellowstone National Park, but the only comparison drawn is that the Yellowstone project demonstrated that canids can successfully re-establish following reintroduction. Newsome et al. (2015) argued that the ecological research in Yellowstone was limited by the lack of detailed studies prior to grey wolf arrival. To avoid ongoing debates (see Peterson et al., 2014), it is therefore crucial that studies in Australia incorporate pre-manipulation monitoring as well as treatment and nil-treatment sites. But at no point do Newsome et al. (2015) state that because grey wolves caused a trophic cascade, dingoes will do so too, or if they do that it will manifest in the same way. Thus, Morgan et al. (2016) provide useful background on the reintroduction of grey wolves into Yellowstone National Park and the interaction pathways affecting this system’s trophic dynamics, and in turn, the applicability of that model to arid and semi-arid Australia. However, their analogy isn't relevant to the case for dingo reintroduction made by Newsome et al. (2015).

The different pathways by which dingoes could influence ecosystems via trophic cascades

Morgan et al. (2016) focused primarily on the dingo-herbivore prey-plant trophic cascade pathway, but only briefly mentioned the dingo-mesopredator-small prey pathway. This was a missed opportunity because both pathways need to be fully considered before evaluating the merits of dingo reintroduction in Australia. We acknowledge that more work is needed to fully disentangle the dingo-herbivore prey-plant pathway, but research on interactions between dingoes, mesopredators and prey is more advanced; see for example Gordon and Letnic (2016); Greenville et al. (2014); Letnic et al. (2009); Letnic and Dworjanyn (2011) and Wang and Fisher (2012). These studies, among others, show that dingoes can suppress or alter the behaviour of mesopredators, and net benefits can accrue for some native species (see Letnic et al. 2009; 2012). Moreover, recent studies provide compelling evidence that the dingo-mesopredator-small prey pathway extends to a fourth trophic level, shrubs, which in the absence of dingoes are released from a recruitment bottleneck imposed by rodents and rabbits (*Oryctolagus cuniculus*) (Gordon et al., 2017; Gordon and Letnic, 2016). Therefore a case could be made to undertake dingo reintroductions based on examination of this trophic cascade pathway alone. Red foxes and feral cats have been implicated in the extinction of at least 20 native mammal species since their arrival in Australia, and both predators currently threaten many extant native species (Woinarski et al., 2015). If reintroducing the dingo can help to slow the attrition of native species and arrest undesirable long-term shifts in woody shrub cover, then there is a very strong case to act now.

Literature and theory relevant to understanding the interplay of bottom-up and top-down processes

The idea that bottom-up processes affect trophic cascades in Australia is not new, and Morgan et al. (2016) omitted relevant studies in this regard. Greenville et al. (2014) examined spatial and temporal interactions between dingoes, red foxes and feral cats. Their study assessed whether bottom-up interactions can regulate sympatric predator populations in environments that experience resource pulses. Consistent with theory and predictions, the authors found that dingoes suppress the abundances of both species, but that these effects are strongest during declines and busts in prey numbers. This study could have been discussed by Morgan et al. (2016) when they stated that "interactions between them [dingoes, red foxes and feral cats] ... are unclear". Furthermore, the study by Greenville et al. (2014) highlighted that because of Australia's variable climate, the dingo has an integral role to play. They note "given that resource pulses are usually driven by large yet infrequent rains, we conclude that top predators like the dingo provide net benefits to prey populations by suppressing mesopredators during prolonged bust periods when prey populations are low and potentially vulnerable". Thus, even if interactions between dingoes and mesopredators differ from those observed among Yellowstone's carnivore guild (as Morgan et al. 2016 point out), this does not mean they do not exist.

Another study examines how variation in primary productivity modulates the suppressive effects of dingoes on kangaroos. Letnic and Crowther (2013) examined the applicability of the Exploitation Ecosystems Hypothesis (EEH) to arid environments in Australia by comparing indices of kangaroo abundance along a rainfall gradient in areas where dingoes were rare versus common. The EEH predicts that herbivore biomass should increase linearly with primary productivity in the absence of predators; but when predators are present, herbivore biomass will remain relatively constant due to top-down regulation (Letnic and Crowther, 2013). Letnic and Crowther (2013) found that kangaroo populations are primarily top-down regulated in the presence of dingoes, and argue that top-down forcing can prevail over bottom-up regulation of herbivore populations in arid Australia. The omission of Letnic and Crowther (2013) by Morgan et al. (2016) is puzzling as it is one of the most recent studies testing the relationships between dingoes and kangaroos in arid Australia, and the results contradict statements that “dry conditions commonly cancel any predator effects”.

Moving the debate forward

The reintroduction of grey wolves into Yellowstone National Park provides many lessons. This management action is a high profile case study that has generated extensive research, but also debate about the ecological role of grey wolves as an apex predator. Because of this, the Yellowstone research is frequently cited. However, proposals to reintroduce dingoes into Australia have never been based on Yellowstone research alone. They have been based on accumulating evidence that apex predators (including dingoes) can have a strong influence on the structure of ecological assemblages (Caughley et al., 1980; Colman et al., 2014; Dickman et al., 2009; Estes et al., 2011; Letnic et al., 2009; Newsome, 2001; Newsome et al., 2015; Ripple et al., 2014; Ritchie and Johnson, 2009). Under the definition of Ripple et al. (2016), trophic cascades are indirect species interactions that originate with predators and spread downward through food webs. In order to determine whether a trophic cascade exists, Ford and Goheen (2015) argued that the direction and strength of interactions between trophic levels need to be quantified individually. Dingoes can and do cause trophic cascades under the definition of Ripple et al. (2016); see for example Gordon et al. (2015). The direction and strength of interactions between dingoes and species at other trophic levels have also been examined and quantified; see for example Gordon and Letnic (2016), Letnic et al. (2009), and Wallach et al. (in press).

Although we disagree with the analogy and arguments made by Morgan et al. (2016), we acknowledge the need for further studies assessing the ecological role of the dingo in Australia. However, it is puzzling that Morgan et al. (2016) have essentially argued that dingo reintroduction proposals are flawed, when some of these same authors (GAB, PJSF) were co-authors of Newsome et al. (2015) and have argued in other publications (e.g. Allen et al. 2013) that manipulations of dingo abundance like the one proposed by Newsome et al. (2015) are priorities for assessing whether dingo removal adversely affects ecosystem processes.

To date, most studies assessing the ecological role of the dingo have involved comparisons of ecological attributes or manipulations of species at lower trophic levels in areas where dingoes are present versus rare or absent, or in areas where dingoes are controlled versus not controlled (Letnic et al., 2012; Gordon and Letnic 2016; Gordon et al. 2015). While these have been (and continue to be) useful in many ways, there is no better way to test how the dingo affects ecosystems than actually reintroducing them into areas where they persist at low numbers or have been extirpated. In their reply, we would therefore encourage Morgan et al. (2016) to comment on whether we should continue to conduct the same research under the same experimental design, or whether we should undertake bold steps via dingo reintroductions.

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