Are wolves just wasps with teeth? What invertebrates can teach us about mammal top predators

Amanda J. Meadows *, David W. Crowder, William E. Snyder

Department of Entomology, Washington State University, Pullman, Washington 99164, USA

ARTICLE INFO

ABSTRACT

Manipulative experiments are rarely possible with large predatory mammals. However, field manipulations of predatory arthropods are common and could provide general insights into top-predator impacts. For example, observational studies suggest that conserving dingoes might indirectly benefit Australian small mammal populations. This is consistent with the effects of praying mantids in eastern U.S. meadows, where mantids indirectly benefit smaller herbivores by eating herbivorous competitors and dangerous mesopredators. However, in other cases predatory arthropods yield only occasional or context-dependent benefits to smaller prey, or even harm them; this suggests caution in assuming universal benefits of dingo conservation. Likewise, some experimental manipulations of predatory arthropods suggest that increasing plant diversity could protect African wild dogs from larger predatory mammals that steal their prey. However, other studies suggest that mesopredators may actually be harmed when the foraging environment becomes more complex. Finally, work with predatory spiders supports the idea that wolves, newly restored to the western U.S., might indirectly benefit some native plants by altering herbivore foraging patterns. However, other work suggests indirect, behaviorally-mediated effects on prey and plants that fall well outside of this type of simple, linear predator-herbivore-plant interaction chain. In summary, top predators that differ in size by orders of magnitude might impact their communities in broadly similar ways. At the same time, work with predatory arthropods indicates that subtle differences in ecological context can yield broadly different outcomes that also must be considered during top-predator conservation.

© 2016 Elsevier Inc. All rights reserved.

Contents

1. Introduction

Worldwide, many species of carnivorous mammals have experienced population declines due to habitat fragmentation, range restriction, and human persecution (Ceballos and Ehrlich, 2002; Ripple et al.,

2014). These losses have kindled interest in the ecological consequences of removing top predators. Studies comparing ecosystems with or without top predators often show that predator-loss degrades critical ecosystem functions such as carbon storage, biodiversity maintenance, and disease regulation (Estes et al., 2011; Ripple et al., 2014). These changes likely stem from the dual effects of large predators on smaller mesopredators and their shared herbivore prey through both lethal (e.g. Gordon et al., 2015; Mills and Gorman, 1997) and non-lethal

means (e.g. Fortin et al., 2005; Vanak et al., 2013). That is, top predators impact mesopredators and herbivores by eating them and by triggering costly predator avoidance behaviors (Preisser et al., 2005; Werner and Peacor, 2003). In turn, conservation of top predators could help restore or maintain ecosystem function and stability (Ritchie et al., 2012; Ritchie and Johnson, 2009). However, experimentally manipulating top carnivores to directly test impacts on mesopredators and herbivores is notoriously difficult because of the large size and ranges of these species, and ethical concerns associated with instituting experiments that could harm endangered animals (Colman et al., 2014; Duffy, 2002). As a result, the majority of studies attempting to describe the regulatory role of mammal top predators are observational (Mech, 2012; Allen et al., 2014, 2015).

Fortunately, experimentally-tractable arthropod communities contain top predators that feed on intermediate predators and herbivore prey. Arthropod predators can initiate strong top-down effects that influence ecosystem structure and function (Duffy, 2002). Furthermore, arthropod predators also suffer biodiversity losses in degraded ecosystems (Kruess and Tscharntke, 1994). Decreased arthropod-predator richness in degraded habitats, such as agricultural fields (e.g., ColungaGarcia et al., 1997), has raised questions about the role of small-predator biodiversity in pest suppression (Cardinale et al., 2003; Ives et al., 2005; Letourneau et al., 2009; Straub et al., 2008). The small size and relaxed ethical considerations associated with arthropods also allow ecologists to perform robust experiments to critically examine these predators' ecological roles.

Here, we argue that when arthropod and mammalian top predators are situated atop similarly-structured food webs, arthropod systems provide a frame-of-reference for studying mammalian systems. Experiments with predatory arthropods allow ecologists to carefully isolate particular factors mediating results, thus providing insight about how top predators impact communities. We acknowledge that while large predatory arthropods are the "top predators" in the context of the community of smaller arthropods that serve as their prey, they can be preyed upon by other predatory vertebrates (e.g., Polis, 1991) and thus are not true top predators (sensu Wallach et al., 2015). We will discuss three large-predatory-mammal conservation issues where progress has been hindered by a lack of data from rigorous, manipulative experiments. In each case, we describe a similarly-structured community of predatory arthropods where experimental data are in hand. Results from the arthropod food webs provide insights that might improve conservation efforts in the analogous large-mammal system. The conservation needs we address are: (1) determining whether dingo (Canis lupus dingo) restoration is likely to bolster

small-mammal numbers in Australia; (2) identifying strategies to protect the African wild dog (Lycaon pictus), an endangered mesopredator on African savannas, from depredations of larger top predators; and (3) developing a comprehensive assessment of how wolf (Canis lupus) re-introduction to the western U.S. will alter foraging behavior, and ultimately densities, of other large mammals. We close by considering how communication between ecologists studying predators that are very large, and those that are quite small, might benefit both parties.

2. Are dingoes just praying mantids with teeth?

In Australia, invasive mesopredators such as red foxes (Vulpes vulpes) and feral cats (Felis catus) can prey heavily upon, and thus threaten, many small native mammals (McKenzie et al., 2007; Davis et al., 2015). Dingoes (Canis lupus dingo) are the only remaining terrestrial top predator in Australia (Johnson, 2006), and are thought to possibly benefit small mammals through two distinct, indirect channels (Fig. 1A). First, dingoes kill and eat large, herbivorous kangaroos (Macropus spp.) and other herbivores that potentially compete with smaller native herbivores for shared food plants and remove plant-cover relied upon by smaller native mammals for shelter (Fig. 1A) (Wallach et al., 2010; Letnic et al., 2012). By preying on herbivores, dingoes thus provide an indirect benefit to smaller native mammals by relaxing resource competition. Second, dingoes kill (and otherwise antagonize) foxes and feral cats, reducing predation of smaller native mammals by these introduced mesopredators (Fig. 1A) (Mitchell and Banks, 2005; Moseby et al., 2012). Of course, at the same time, dingoes also kill and eat the same small mammals as foxes and cats (Fig. 1A) (Mitchell and Banks, 2005; Davis et al., 2015), which might counteract any indirect benefits dingoes provide to small mammals.

Fortunately, a large-scale manipulation of dingoes has provided insight into their potential impact on small native mammals, albeit with some limitations. The top predators were once extirpated from about 25% of Australia to protect livestock (Letnic and Koch, 2010; McKnight, 1969) using a >5000-km fence. Dingoes are generally rare in the rangelands of southeastern Australia, on the exclusion side of the fence, but maintain healthy populations past the fence line (Newsome et al., 2015). On the side of the fence where dingoes remain, observational studies have reported decreased mesopredator abundance, increased small mammal abundance and/or diversity, and decreased densities of large-bodied native herbivores (e.g. Letnic et al., 2009a; Letnic et al., 2009b; Letnic and Dworjanyn, 2011; Pople et al., 2000; Wallach et al., 2010). This pattern has led some to claim that dingoes indirectly benefit conservation of small native mammals; if
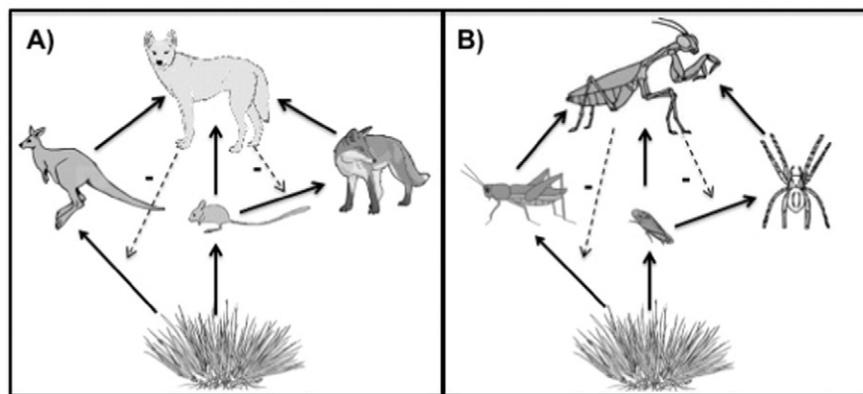

Fig. 1. In Australia, simple comparisons of mammal communities with and without top predators suggest that (A) dingoes may benefit small mammal populations indirectly, by consuming kangaroos and other large herbivores that compete with the small mammals, or by consuming foxes and other exotic mesopredators that eat them. However, dingoes also consume small mammals, a direct harm that may counterbalance any indirect benefit. In eastern U.S. old-field-arthropod communities, manipulative field experiments have demonstrated that (B) praying mantids benefit smaller herbivorous insects both by eating larger-herbivore competitors, and by eating (and otherwise interfering with) wolf-spider mesopredators that are the key predators of smaller herbivores; the net cascading effect of mantids is to increase overall plant biomass. We suggest that, given the similar trophic structures across the two communities, lessons learned with praying mantids could prove relevant to small-mammal management in Australia. Solid arrows indicate the flow of energy through the food web. Dashed arrows indicate the effect the species at the origin has on the indicated interaction; labels indicate whether this species strengthens (+) or weakens (−) the interaction.

this is correct, any harm to small mammals from dingo predation is of relatively minor consequence (Letnic et al., 2009a; Nimmo et al., 2015; Ritchie et al., 2012). This suggests that restoring dingoes to areas where these predators are currently excluded could be a critical first step towards the restoration of robust small-native-mammal populations (Nimmo et al., 2015; Ritchie et al., 2012).

However, other ecologists are more cautious about assigning dingo presence as the cause of these patterns given multiple alternative explanations not considered by previous studies (e.g., Allen et al., 2013; Newsome et al., 2001). Efforts to infer dingoes' impacts are also limited by confounding factors that differ across sides of the fence, including that dingo exclusion focused on protecting the most productive grazing lands (McKnight, 1969), establishing a potentially confounding productivity difference. Moreover, livestock grazing and associated herbivore communities directly reduce plant cover, possibly establishing a confounding difference in food and shelter resources used by small mammals (Allen, 2011; Smith and Quin, 1996). Large-scale predator manipulation experiments (without fence effects) have also consistently yielded evidence that dingoes do not elicit the cascading effects predicted by earlier cross-fence observational studies (Eldridge et al., 2002; Allen et al., 2013, 2014). Furthermore, it remains unclear whether any impacts of dingoes cascade to benefit plant biomass or biodiversity given other unaddressed historical facts (Cooke and Soriguer, 2017; Glen et al., 2007). Additional experimental manipulations of livestock grazing and dingo presence/absence, across well-replicated sites, could resolve some of these controversies. In the absence of further rigorous experimental data, large-scale restoration of dingo populations may be premature, some authors have warned, given the known costs of dingoes to livestock production and likelihood that dingoes will prey directly on endangered small mammals (Glen, 2012; Allen et al., 2013; Hayward et al., 2015; Hayward and Marlow, 2014). Clearly, the net effect of dingoes on sensitive small mammals is complex (Cooke and Soriguer, 2017; this issue), possibly dependent on the specific ecological context being considered (Haswell et al., 2017), and not easily unraveled without manipulative field experiments (Allen et al., 2013).

Fortunately, the types of experimental predator manipulations so difficult with dingoes are regularly conducted within arthropod communities. This raises the intriguing possibility that, if communities of predatory arthropods and their prey can be located that share a basic food web structure with those dominated by dingoes, we might extrapolate from the arthropods to predict how dingoes may affect their communities. Such a system is the community of "old field" (i.e., retired agricultural fields now colonized by grasses and forbs) arthropods topped by predatory, non-native Chinese praying mantids (*Tenodera sinensis*) in the eastern U.S. (Snyder and Hurd, 1995). The mantids are the largest arthropod predators in these communities, and feed on both wolf spider (*Rabidosa rabida*) mesopredators and a rich community of herbivorous insects (Fig. 1B). Therefore, the basic trophic structure is similar to Australian dingo-topped communities (Fig. 1). In turn, this potentially sets the stage for the same complex mix of indirect benefits, and direct harms, that mantids might exert on herbivorous insects (which are trophically analogous to the Australian native smaller mammals that conservation efforts seek to benefit) (Fig. 1).

Hurd and colleagues have conducted a series of experimental manipulations where replicate plots are established to contain or exclude Chinese mantids; thereafter direct and indirect effects of the mantids on herbivores and plants are tracked throughout the growing season (e.g., Hurd and Eisenberg, 1984; Moran and Hurd, 1998; Moran et al., 1996). These manipulations have revealed several clear and consistent patterns. First, mantids reduce densities of the wolf spiders that are the main mesopredators in the system through direct consumption (Moran and Hurd, 1994). The mantids also induce predator-avoidance behaviors whereby spiders emigrate out of plots with mantids, which reduces mesopredator densities through non-lethal means (Moran and Hurd, 1994; Moran et al., 1996). Mantids' impacts on herbivorous

insects are more complex: in the presence of mantids overall herbivore biomass decreases, but total herbivore abundance is unchanged (Hurd and Eisenberg, 1984; Moran and Hurd, 1998). This puzzling result appears to reflect mantids preferentially preying on the largest herbivorous insects (Moran and Hurd, 1994, 1998). Mantids appear to (1) largely ignore smaller herbivores as prey, and (2) free smaller herbivores from predation by wolf spiders, increasing small-herbivore numbers sufficiently to compensate for reduced numbers of larger herbivores while reducing overall herbivore biomass (Hurd and Eisenberg, 1984; Moran and Hurd, 1998). Importantly, mantids also trigger a powerful trophic cascade leading to greater total plant biomass (Moran and Hurd, 1998) (Fig. 1B).

Therefore, results from the mantid system suggest that dingo restoration could indeed encourage small-mammal populations in Australia by (1) decreasing competition among large and small herbivore species, (2) suppressing mesopredators and thus relaxing predation on smaller prey species, and (3) indirectly increasing plant biomass to the benefit of Australian native plant communities (e.g., Glen et al., 2007; Letnic et al., 2009b). However, such an outcome would rely on dingoes suppressing foxes and cats, and dingoes preying predominately on larger herbivores, which does not always appear to be the case (Allen et al., 2013; Allen and Leung, 2015). Indeed, the specific ecological interactions that typify the mantid system, where large predators eats small predators and larger herbivores, freeing smaller herbivores from predation and competition, appears to be somewhat of a rare phenomenon. Perhaps as often, arthropod top- and mesopredators combine to detrimentally impact both large and small herbivores, triggering a broad trophic cascade that benefits plants (Duffy et al., 2005; Hooper et al., 2005; Letourneau et al., 2009). For example, herbivorous insects that feed on *Brassica oleracea* plants are attacked by a diverse community of predatory arthropods (Snyder et al., 2006; Straub and Snyder, 2006; Northfield et al., 2010; Steffan and Snyder, 2010; Gable et al., 2012). The predators include larger predators (such as lady beetles) that regularly prey upon some of the smaller predators (such as parasitoid wasps). The herbivore community includes both caterpillars, which are relatively large, and relatively small phloem-feeding aphids that presumably compete with the caterpillars. So, the trophic structure nicely reproduces the mantid and dingo communities (Fig. 1), and one might expect top predators to exert similar impacts in each system. This is not the case, however (Fig. 3B). Indeed, field experiments show that top- and mesopredators combine to suppress densities of both caterpillars and aphids (Snyder et al., 2008; Straub and Snyder, 2006; Northfield et al., 2010; Steffan and Snyder, 2010; Gable et al., 2012). This is because the small and large predators differ in where they hunt for prey on the plants (Straub and Snyder, 2006; Gable et al., 2012), and thus combine to kill more herbivores than could any single predator species on its own (Northfield et al., 2010). That is, top- and mesopredators occupy different, and complementary, niches (Northfield et al., 2010). Top predators do regularly eat mesopredators in this community, but effects of intraguild predation are generally weak and thus mesopredators generally benefit from being among top predators (Takizawa and Snyder, 2011a,b).

A broader look at the literature suggests that arthropod top predators have widely variable impacts on relatively small prey species. The best-case scenario (from the standpoint of the small prey) is that the large predator focuses its attacks on mesopredators and competing larger herbivores, largely ignores smaller herbivores, releasing the smaller herbivore from competition and predation (e.g., Finke and Denno, 2004). However, it appears that in many cases the net impact of predators is similar for small and large herbivores, leading to overall lower herbivore densities and increased plant biomass (e.g., Duffy et al., 2005; Hooper et al., 2005; Letourneau et al., 2009). This is because complementarity among different predator species is common (Ives et al., 2005; Straub et al., 2008). In contrast, powerful intraguild predation that protects herbivores from predation by mesopredators, in the absence of the top predator, is likely relatively rare (Ives et al., 2005; but see Polis et al., 1989; Polis and Holt, 1992). Beyond this, insect ecologists

have long debated whether herbivore species commonly compete with one another (e.g., Denno et al., 1995; Hairston et al., 1960). This means that top predators that kill larger competing herbivores will not necessarily provide a beneficial relaxation of herbivore-herbivore competition.

In summary, we suggest that several factors influence whether top predators are likely to have a net positive or negative impact on vulnerable small prey species, such as those that dingo conservation advocates are seeking to protect. First, we must consider the degree to which the target for protection is preyed upon by the top versus intermediate predator; if the top predator feeds heavily on the endangered prey species then top predators will, on the whole, harm that prey (e.g., Snyder et al., 2008). Second, the degree to which the top predator attacks the mesopredator is important. When the top predator heavily limits the mesopredator's abundance this can relax predation on the prey (e.g., Finke and Denno, 2004). However, when this intraguild predation is relatively weak, the larger and smaller predators may primarily complement one another by occupying different niches and thus combine to increase predation of the prey (e.g., Snyder et al., 2006; Gable et al., 2012). Finally, it cannot be assumed that smaller prey species necessarily compete with one another (e.g., Denno et al., 1995); this is something that must be verified before assuming that removing larger prey species necessarily benefits smaller ones. Of course, all of the above factors might vary independently from one another, with the potential to height context-dependence of top predators' net effects on particular prey species. Indeed, effects of a particular top predator species have been shown to vary across landscapes, reflecting changes in ecological context from one site to another (e.g., Grez et al., 2014).

3. Are lions just wolf spiders with teeth?

African savannas can support a diverse carnivore guild, including larger predators such as lions (*Panthera leo*), leopards (*Panthera pardus*), cheetahs (*Acinonyx jubatus*) and spotted hyenas (*Crocuta crocuta*) (Fig. 2A). Co-existing with these top predators are mesopredators such as African wild dogs (*Lycaon pictus*) (Radloff and Toit, 2004) (Fig. 2A). Because of human persecution and habitat fragmentation, most viable populations of these carnivores persist in fenced reserves (Darnell et al., 2014). While prey may not be limiting in these protected areas, they bring predators into closer proximity than would be expected for free-ranging populations (Darnell et al., 2014). This is problematic because spatial avoidance is a key way that African wild dogs avoid kleptoparasitism (the theft of their prey) and intraguild killing by the larger predators (Caro and Stoner, 2003; Gorman et al., 1998; Van Der Meer et al., 2011; Vanak et al., 2013). Indeed, lions and hyenas sometimes steal more than a third of all African wild dog prey-kills (Gorman et al., 1998), endangering the dogs' long-term survival. Intriguingly, however, levels of kleptoparasitism are notably lower in wooded areas (Creel, 2001; Creel and Creel, 1998). One possible explanation is that the increased structural complexity of forests makes it more difficult for dominant top predators to locate and steal the prey of wild dogs (Creel, 2001) (Fig. 2A). However, this has never been rigorously examined, and likely could never be experimentally tested given the obvious difficulty in conducting a fully-factorial manipulation of both large predator presence/absence and the presence/absence of complex woody vegetation, and the severely-endangered status of most wild-dog populations (Swanson et al., 2014).
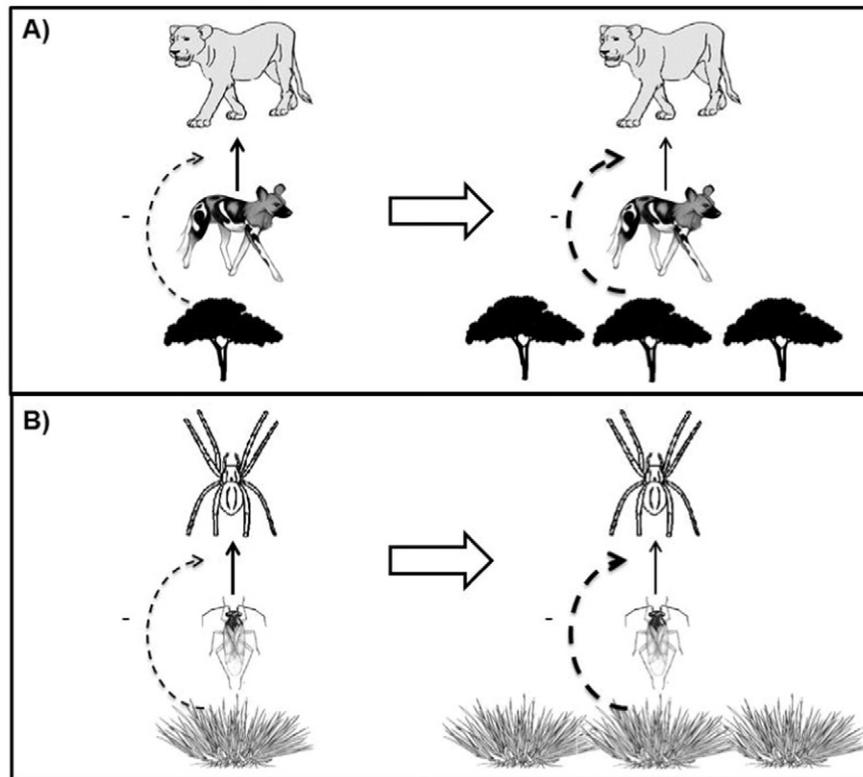

Fig. 2. Within African-savanna preserves, (A) lions and other top predators harm African wild dogs, mesopredators of conservation concern, by stealing the dog's prey and occasionally eating dogs (left side of panel A); however lion-dog antagonism appears to be relaxed in forested preserves that provide wild dogs with additional cover (right side of panel A). In eastern-U.S. salt marshes, manipulative field experiments have demonstrated that (B) in structurally simple environments, wolf-spider top predators decimate populations of predatory-bug mesopredators that otherwise limit densities of planthopper herbivores that damage cordgrass (left side of panel B); experimental addition of dead-grass thatch reduces predator-predator antagonism, allowing a trophic cascade where predatory bugs suppress the herbivores and promote stronger plant growth (right side of panel B). We suggest that in both systems greater structural complexity reduces encounters between top- and mesopredators, shielding the mesopredators from top predators. Solid arrows indicate the flow of energy through the food web. Dashed arrows indicate the effect the species at the origin on the indicated interaction; labels indicate whether this species strengthens (+) or weakens (−) the interaction. The weight of the arrow is proportional to the strength of the effect.

Fortunately, arthropod ecologists have explored how habitat structural complexity mediates interactions among predators. This research suggests generally-applicable principles for where and how structural complexity may dampen predator-predator antagonism. In arthropod communities in agricultural systems, the goal typically is to maximize total density of predatory arthropods that control pests (Langellotto and Denno, 2004). As in savanna preserves where predatory mammal species are brought into close contact, in agricultural fields a surprisingly diverse community of predatory bugs, beetles, and spiders often co-exist in small areas (Ives et al., 2005; Straub et al., 2008). This co-occurrence provides many opportunities for predators to feed on one another, and in extreme cases intraguild predation disrupts biological control and triggers herbivore outbreaks (e.g., Rosenheim et al., 1993; Finke and Denno, 2004; Pell et al., 2008). Disrupted biological control is most common when relatively large predators attack and kill relatively small predators that are the key pest regulators (Ives et al., 2005). This occurs because, like the African dogs, smaller predatory arthropods are particularly susceptible to the depredations of their larger competitors (Polis et al., 1989; Straub et al., 2008). So, it appears that we have again located a situation where insect ecologists have considered questions roughly analogous to the large-mammal-predator system that is of conservation interest.

Interestingly, as has been suggested but not demonstrated for African wild dogs, antagonism among arthropod predators appears often to be dampened in structurally-complex environments (Langellotto and Denno, 2004). Perhaps the best example of this comes from cordgrass (*Spartina* spp.) communities in eastern-U.S. marine estuaries (Fig. 2B). Growth of the grasses can be stunted through feeding by *Proklesia* planthoppers; these herbivores are regulated by *Tytthus* predatory bugs that devour planthopper eggs (Finke and Denno, 2004) (Fig. 2B). This trophic cascade is endangered by *Pardosa* wolf spiders, top predators that feed heavily on the mesopredator *Tytthus* but only weakly on the herbivore *Proklesia*. In lower-marsh areas where the ground is largely free of plant debris, spiders decimate the mesopredators and indirectly trigger planthopper outbreaks which reduce cordgrass biomass (Finke and Denno, 2004, 2005) (Fig. 2B). Interactions are quite different, however, higher in the marsh where a thick layer of dead-cordgrass "thatch" creates a complex foraging environment (Fig. 2B). In a series of field and greenhouse experiments, Denno et al. (2002) manipulated densities of wolf spider top-predators in the presence or absence of a thatch layer (also see Finke and Denno, 2002). They found that, as in the lower marsh, in the absence of thatch wolf spiders depressed mesopredator numbers, releasing planthoppers from top-down control and heightening herbivory (Fig. 2B). In stark contrast, in the presence of thatch predator-predator interference was reduced, *Tytthus* mesopredators thrived, planthoppers were suppressed, and plants were largely protected (Finke and Denno, 2002). Apparently, thatch reduced encounters between wolf spiders and the predatory bug, but did not substantially disrupt *Tytthus* predation of planthopper eggs, maintaining a strong trophic cascade (Finke and Denno, 2002) (Fig. 2B).

In a meta-analysis analyzing studies involving arthropods, Langellotto and Denno (2004) found seven of nine natural enemy guilds (hunting spiders, web-building spiders, all spiders, mites, true bugs, parasitoids, and ants) were more abundant when habitat complexity increased. This suggests that interference among predatory arthropods generally dampens as environmental complexity increases, as seen in the cordgrass system. Altogether, results from arthropod communities suggest that increasing habitat complexity may a way to increase coexistence between predators and conserve African wild dogs (Fig. 2). This is an alternative strategy to the recommendation to focus wild-dog conservation efforts in areas where competitor populations are already low (e.g., Creel and Creel, 1996; Mills and Gorman, 1997). Indeed, a roughly analogous effect appears to facilitate coexistence among endangered San Joaquin kit foxes (*Vulpes macrotis mutica*) and coyotes (*Canis latrans*) in shrublands of central California, U.S. (Nelson et al., 2007).

There, burned areas create a complex habitat: top-predator coyotes prefer unburned shrubland, while kit foxes find refuge in grasslands opened by fire (Nelson et al., 2007).

Of course, increasing structural complexity will not invariably protect mesopredators from attack by top predators, and work with predatory arthropods suggests important caveats. Key among these is the observation that increasing plant diversity often leads to a concomitant increase in herbivore diversity and/or the diversity/abundance of detritus-feeding species. When these new herbivores or detritivores serve as prey to top predators, impacts on mesopredators can be complex. One of the best-known examples of this is so-called "apparent competition", where the presence of one prey species builds densities of predators that also feed on a second prey species (Chase et al., 2002; Holt and Lawton, 1994). When this occurs, the buildup in predators on the first prey species can increase impacts on the second prey species (e.g. Prasad and Snyder, 2006; Ramirez and Rubanks, 2016). For example, polyphagous big-eyed bugs (*Geocoris punctipes*) foraging on *Phaseolus lunatus* plants feed on both beans produced by the plant, and on damaging caterpillar herbivores (Eubanks and Denno, 1999, 2000). For individual big-eyed bugs, the presence of beans draws the bugs to feed on plant material and protects the caterpillars from predation (Eubanks and Denno, 1999). However, at the community level, beans attract large numbers of predators; as predator densities increase the net impact of beans is to increase attacks on caterpillars (Eubanks and Denno, 2000). This specific case study did not examine a community that included both top and mesopredators, but we can extrapolate to the general case where increasing densities of top predators in response to additional prey, could then indirectly increase top-predator impacts on mesopredators.

In summary, when the prey one is seeking to protect competes strongly with other prey species, and the top predator preferentially attacks these competitors without the predator itself increasing in density, this can benefit the protection target (e.g., Moran et al., 1996). However, when the second prey species builds densities of predators that then also attack the prey species one is seeking to protect, apparent competition can lead to net negative effects on the protection target (e.g., Eubanks and Denno, 1999, 2000). From the standpoint of whether African wild dogs would truly benefit from greater vegetational diversity within preserves, then, we must consider both (1) the degree to which the dogs directly benefit from a structural refuge against encounters with top predators, and (2) whether adding trees to the landscape builds the overall base of prey used by top predators, which could build top predator densities and thus indirectly increase encounters between top and mesopredators.

4. Are wolves just lady beetles with teeth?

Quaking aspen (*Populus tremuloides*) biomass in Yellowstone National Park, in the western U.S., has declined over the past century (Ripple et al., 2001). Many factors including fewer fires (Romme et al., 1995), a drier climate (Romme et al., 1995), and increased elk (*Cervus canadensis*) herbivory (Ripple et al., 2001) have been implicated in this decline. However, evidence has grown that the extirpation of grey wolves (*Canis lupus*) from Yellowstone, in the early 1900s, has played a key role in aspen dynamics (Ripple and Larsen, 2000). Indeed, following reintroduction of wolves in the 1990s, it has been shown that wolves not only reduce numbers of elk, directly protecting aspen from herbivory, but also change elk behavior to the indirect benefit of aspen recruitment (Fig. 3A) (Fortin et al., 2005; Laundre et al., 2001; Ripple et al., 2001; Ripple and Beschta, 2007). Wolves target and effectively hunt elk in aspen groves in the winter, driving elk to the relative safety of coniferous forests (Fortin et al., 2005). Decreased elk browsing in risky aspen stands corresponds to higher mean new stem growth (Ripple et al., 2001; Ripple and Beschta, 2007) and, eventually, recovery of aspen stands (Beschta and Ripple, 2009). Therefore, while wolves do prey directly on elk and initiate a trophic cascade through this lethal
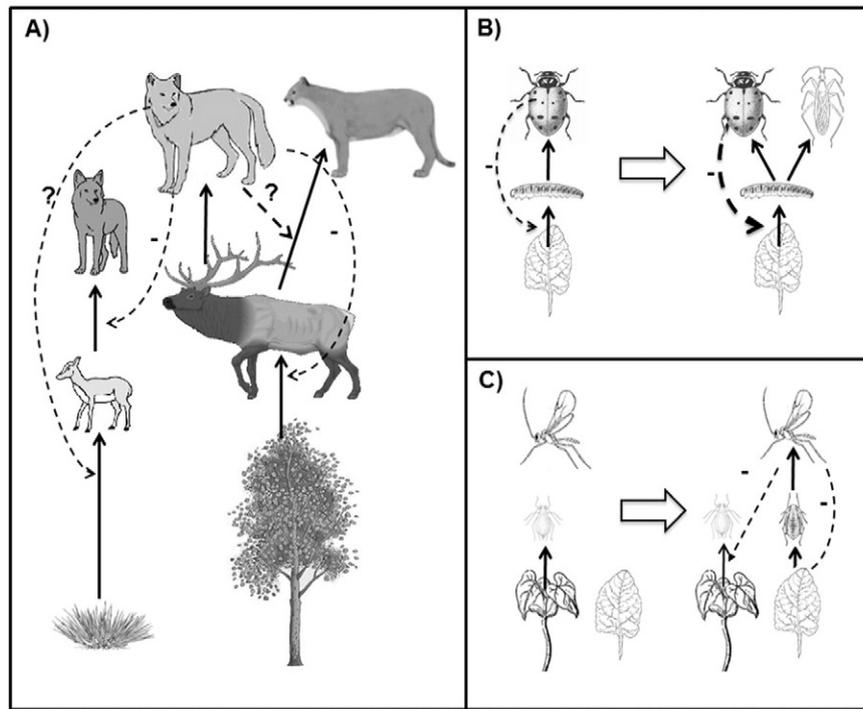
Fig. 3. Wildlife ecologists are beginning to consider how (A) wolf impacts might radiate out, through both lethal and non-lethal channels, to impact community members outside of elk and aspen; additionally-impacted community members could include other top predators such as mountain lions, mesopredators such as coyotes, additional large-mammal herbivores such as pronghorn, and other plant species such as the grasses and forbs upon which pronghorn feed. Work in arthropod systems suggests that these behaviorally-mediated wolf effects might be far-reaching. For example, work in brassica-arthropod sytems (B, C) indicate that predators often initiate behavioral changes in other species, that in turn can impact herbivores and plants in suprisingly complex ways. For predators attacking caterpillars on collard plants, predaotrs were more likely to visit plants when predator communities were species-rich. This translated into more predator-avoidance behaviors and fewer feeding opportunities by the caterpillars (B). The parasitoid *Aphidius colemani* attacks only the green peach aphid, however, a greenhouse experiment revealed that *A. colemani* also unexpectedly reduced pea aphid populations when they co-occur with green peach aphid. The presence of green peach aphid initiates greater foraging effort by *A. colemani*, causing pea aphids to drop from plants and feed less, despite no actual risk posed by the wasp (C). Dashed arrows indicate the effect the species at the origin on the indicated interaction; labels indicate whether this species strengthens (+), weakens (−), or has poorly understood effects (?) on the interaction. The weight of the arrow is proportional to the strength of the effect.

channel, the key benefit of wolves to aspen may be mediated through elk behavioral changes that impact far more elk than wolves can actually kill (Fortin et al., 2005; Ripple and Beschta, 2004). This non-lethal effect of wolves is one of the best-known examples of how predators might indirectly protect plants through behavioral, rather than trophic, means (Ripple et al., 2014).

A clear analog to the wolf-elk-aspen system is seen in work by Schmitz and colleagues with a community of predatory spiders feeding on herbivorous grasshoppers in old-field communities (Schmitz, 1998; Schmitz et al., 1997; Uriarte and Schmitz, 1998). The grasshoppers gain greatest nutrition from feeding on grasses (*Poa* spp), but the herbivores face the greatest threat of being eaten by spiders when on these plants. Therefore, when spiders are present the grasshoppers switch to feeding on goldenrod (*Solidago* spp.), despite those plants' lower food value, and thus the slower growth and poorer survival that grasshoppers experience. Over longer time periods, this behaviorally-mediated shift causes increased plant community evenness because the competitively dominant forbs are suppressed by increased grasshopper foraging, while grasses are simultaneously released from heavy grasshopper grazing. Altogether then, Schmitz and colleagues have displayed a case where the indirect effects of predators, resulting from behavioral changes in their prey, can have ecological consequences that are just as strong as those resulting from direct predation (e.g. Schmitz et al., 1997, 2004). This work with arthropods appears to provide direct parallels to the proposed behaviorally-mediated trophic cascades in the wolf-elk-aspen system, supporting the interpretation of interactions within that community of large vertebrates.

As in all cases already discussed, however, the arthropod literature contains a wide variety of other possible interaction chains beyond what may occur in the wolf-elk-aspen system. Indeed, experimental

design limitations and contrary results from other studies suggest that the wolf-elk-aspen story itself may not be clear-cut (Kauffman et al., 2010; Mech, 2012; Middleton et al., 2013; Marshall et al., 2013). For example, much of this work considers behaviorally-mediated trophic cascades to be transmitted mainly through just three species: wolf, elk, and aspen. However, recent work in arthropod food webs indicates that such effects can radiate far beyond such 3-species interaction chains. For example, Steffan and Snyder (2010) examined impacts of simple versus diverse arthropod-predator communities on herbivorous diamondback moth (*Plutella xylostella*) caterpillars (Fig. 3B). The predators protect the *Brassica oleracea* plants on which the caterpillars feed by eating the caterpillars, and through non-trophic channels, by causing the caterpillars to drop onto silken threads to escape predation (caterpillars cannot feed while hanging on threads). In diverse communities, the two predators that most-commonly initiated caterpillar defensive behaviors, *Hippodamia* lady beetles and *Diadegma* parasitoid wasps, were more likely to visit plants when predator communities were species-rich (Fig. 3B). A probable explanation for this is that intraspecific predator interference was relaxed with more predator species. The greater foraging effort by these predators translated into caterpillars dropping from plants more often, which protected plants from herbivory through an indirect and behaviorally-mediated channel (Steffan and Snyder, 2010). Therefore, a modification of predator behavior seen only in multi-species predator communities, heightened the behavioral impact of the predators on herbivores and strengthened the behaviorally-mediated trophic cascade (Steffan and Snyder, 2010) (Fig. 3B). This suggests that top predators can exert behaviorally-mediated impacts that also radiate out among other predator species.

A second example comes from the community of parasitoid wasps that attack aphid pests in polycultures of collard plants (*Brassica*

oleracea) interspersed with plantings of fava beans (*Vica faba*) (Fig. 3C). The collard plants house the green peach aphid, *Myzus persicae*, while the fava bean plants house the pea aphid, *Acyrthosiphon pisum*. The parasitoid *Aphidius colemani* attacks only the green peach aphid, and so would be expected only to indirectly benefit growth of collard plants (Fig. 3C) (Fill et al., 2012). However, a greenhouse experiment revealed that *A. colemani* unexpectedly also reduced pea aphid populations. This apparently occurred because *A. colemani* caused pea aphids to drop from plants, an escape behavior deployed in the presence of a wasp that posed no true risk to that aphid species (Fig. 3C) (Fill et al., 2012). This demonstrates how behavioral impacts of top-predators can "jump food chains", radiating out from one predator-prey interaction to a second prey species that never is trophically impacted by the predator.

Indeed, recent work suggests that wolf effects do indeed radiate beyond the wolf-elk-aspen chain (Berger and Gese, 2007). For example, by suppressing coyote mesopredators, wolves are implicated in releasing pronghorn (*Antilocapra americana*) (Fig. 3A) from heavy neonatal predation by coyotes (Berger et al., 2008). Other possibilities to explore could include determining how behavioral interactions among wolves, grizzly bears (*Ursus arctos horribilis*), mountain lions (*Puma concolor*), and coyotes influences landscape-use patterns of these top and mesopredators, and in turn how this impacts risk perception in a range of herbivore prey including elk, moose (*Alces acles*), mule deer (*Odocoileus hemionus*), and pronghorn. Indeed, each of the predatory mammals can have antagonistic interactions with one another on or even off kills (Berger and Gese, 2007; Gunther and Smith, 2004; Kunkel et al., 1999), reflecting occasional intraguild predation of smaller predators by larger ones (Berger and Gese, 2007; Gunther and Smith, 2004; Kunkel et al., 1999) while the herbivores compete for resources (Singer and Norland, 1994). In turn, such complex behaviorally-mediated interactions might yield unexpected impacts on productivity of different plant species fed on by herbivorous mammals; some plant species may increase while others may decrease. Whether or not this trophic cascade is considered to be beneficial depends on the conservation status of plants involved.

5. Synthesis and future directions

Large- and intermediate-sized predatory mammals, and many of their mammalian prey, are of conservation importance worldwide (Crooks and Soule, 1999; Ripple et al., 2014). However, experimental manipulations of these communities can be difficult or unethical (e.g., Letnic et al., 2009a; Newsome et al., 2015; Sergio et al., 2014). This leaves researchers to infer cause-effect relationships from "natural experiments" where predators are absent from sites they formerly occupied, or through time-consuming field observations of species interactions (e.g., Berger et al., 2008; Colman et al., 2014; Creel and Creel, 1998). In either case, confounding differences between sites where predators remain or are now absent, inevitably complicate clear delineation of top-predator effects and the isolation of cause-effect relationships (Allen et al., 2013; Colman et al., 2014; Mech, 2012). Furthermore, even if large mammalian predator populations were to be restored, it is unclear if they will again provide their full potential of ecosystem services, especially in degraded and fragmented habitats (Fleming et al., 2012).

We suggest that arthropod systems can share similar food web architectures with their larger mammalian brethren, where experimental work with arthropods is relatively straightforward and key experiments often have already been completed. In turn, management decisions with much larger predatory mammals where experimental work is not possible might be informed with results from arthropod systems. For example, wildlife managers in Australia are debating restoration of dingoes to landscapes from which they have been intentionally removed, in an effort to indirectly benefit declining small, native mammals. Experimental work with praying mantis top predators, wolf

spider mesopredators, and large and small herbivorous insects, a trophic structure similar to the dingo system (Fig. 1), suggests that under certain conditions, dingo repatriation might benefit small mammals through the indirect channels (herbivore-competitor and mesopredator reduction) that some wildlife ecologists have long suggested (e.g., Nimmo et al., 2015; Ritchie et al., 2012). However, we must acknowledge that this "best case" outcome is exceedingly sensitive to the strength of each link in the food web; relatively strong predation of top predators on the small native prey (e.g., Crowder and Snyder, 2010), relatively weak predation of mesopredators by top predators (e.g., Snyder et al., 2008), and an absence of competition among prey species (e.g., Denno et al., 1995) all have the ability to *reverse* our predictions about whether top-predator conservation would bring conservation benefits.

Likewise, experimental work with predatory arthropods generally finds reduced predator-predator antagonism in structurally-complex environments (e.g., Amaral et al., 2015; Finke and Denno, 2002), suggesting that African wild dogs might be protected from top-predator antagonism on vegetatively-diverse preserves including woodlands (as suggested by Creel, 2001) (Fig. 2). However, increasing woodland coverage in these preserves to the benefit of prey species risks increasing overall prey availability to, and thus densities of, top predators (e.g., Kozar et al., 1994) to the harm of wild dogs. Finally, diverse behaviorally-mediated interactions are known to radiate widely throughout predatory arthropod communities where multiple predator species are considered simultaneously (e.g., Philpott et al., 2012; Sitvarin and Rypstra, 2014; Steffan and Snyder, 2010) (Fig. 3). Hence, knowledge from arthropod systems suggests wolf reintroduction in the American West will produce behavioral changes in other top- and mesopredators, impacting a broad range of herbivorous mammals and native plants (Ripple et al., 2014) (Fig. 3). Therefore, while some components of the arthropod-predator literature offer support for mammalian conservation schemes that involve altering top predator abundances or behavior, other studies suggest ways that these same efforts might go badly awry. This suggests a cautious approach to moving information from arthropod to mammalian systems, with the potential to understand both possible gains, and possible harms, of particular management schemes.

Movement of insights in the other direction, from mammalian to arthropod systems, might be equally valuable. While arthropod predator-prey work often focuses on manipulative experiments at the scale of plots spanning no more than several square meters (Schmitz, 2005), predator manipulation, exclusion or containment among mammal communities often occurs at a grand scale of tens of thousands of square kilometers (Hayes et al., 2003; Allen et al., 2013; Hervieux et al., 2014); such manipulations might also keep predators in or out of communities for time scales much longer than those considered in most experimental arthropod communities (Borer et al., 2005). For this reason, the mammal studies can provide insights at spatiotemporal scales far beyond what most insect ecologists encompass, potentially highlighting important interactions only seen over broader scales of space and time (e.g., Allen et al., 2013). Our overview of the literature, along with similar previous attempts (e.g., Schmitz, 2005; Sergio et al., 2014), hopefully encourages those interested in predators small and large to continue to maintain a vigorous, active dialog with one another.

References

Allen, B.L., 2011. A comment on the distribution of historical and contemporary livestock grazing across Australia: implications for using dingoes for biodiversity conservation. Ecol. Manag. Restor. 12, 26–30.

Allen, B.L., Leung, L.K.P., 2015. The (non) effects of lethal population control on the diet of Australian dingoes. PloS one 9 (9), e108251.

Allen, B.L., Fleming, P.J.S., Allen, L.R., Engeman, R.M., Ballard, G., Leung, L.K.P., 2013. As clear as mud: a critical review of evidence for the ecological roles of Australian dingoes. Biol. Conserv. 159, 158–174.

Allen, B.L., Allen, L.R., Engeman, R.M., Leung, L.K.-P., 2014. Sympatric prey responses to lethal top-predator control: predator manipulation experiments. Front. Zool. 11, 56.

Allen, B.L., Allen, L.R., Leung, K.-P., 2015. Interactions between two naturalised invasive predators in Australia: are feral cats suppressed by dingoes? Biol. Invasions 17, 761–776.

Amaral, D., Venzon, M., Perez, A.L., Schmidt, J.M., Harwood, J.D., 2015. Coccinellid interactions mediated by vegetation heterogeneity. Entomol. Exp. Appl. 156, 160–169.

Berger, K.M., Gese, E.M., 2007. Does interference competition with wolves limit the distribution and abundance of coyotes? J. Anim. Ecol. 76, 1075–1085.

Berger, K.M., Gese, E.M., Berger, J., 2008. Indirect effects and traditional trophic cascades: a test involving wolves, coyotes, and pronghorn. Ecology 89, 818–828.

Beschta, R.L., Ripple, W.J., 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. Biol. Conserv. 142, 2401–2414.

Borer, E.T., Seabloom, E.W., Shurin, J.B., Anderson, K.E., Blanchette, C.A., Broitman, B., Cooper, S.D., Halpern, B.S., 2005. What determines the strength of a trophic cascade? Ecology 86, 528–537.

Cardinale, B.J., Harvey, C.T., Gross, K., Ives, A.R., 2003. Biodiversity and biocontrol: emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem. Ecol. Lett. 6, 857–865.

Caro, T.M., Stoner, C., 2003. The potential for interspecific competition among African carnivores. Biol. Conserv. 110, 67–75.

Ceballos, G., Ehrlich, P.R., 2002. Mammal population losses and the extinction crisis. Science 296, 904–907.

Chase, J.M., Abrams, P.A., Grover, J.P., Diehl, S., Chesson, P., Holt, R.D., Richards, S.A., Nisbet, R.M., Case, T.J., 2002. The interaction between predation and competition: a review and synthesis. Ecol. Lett. 5, 302–315.

Colman, N.J., Gordon, C.E., Crowther, M.S., Letnic, M., 2014. Lethal control of an apex predator has unintended cascading effects on forest mammal assemblages. Proc. R. Soc. B Biol. Sci. 281, 8.

ColungaGarcia, M., Gage, S.H., Landis, D.A., 1997. Response of all assemblage of Coccinellidae (Coleoptera) to a diverse agricultural landscape. Environ. Entomol. 26, 797–804.

Cooke, B.D., Soriguer, R.C., 2017. Do dingoes protect Australia's small mammal fauna from introduced mesopredators? Time to consider history and recent events. Food Webs 12, 94–105.

Creel, S., 2001. Four factors modifying the effect of competition on carnivore population dynamics as illustrated by African wild dogs. Conserv. Biol. 15, 271–274.

Creel, S., Creel, N.M., 1996. Limitation of African wild dogs by competition with larger carnivores. Conserv. Biol. 10, 526–538.

Creel, S., Creel, N.M., 1998. Six ecological factors that may limit African wild dogs, *Lycaon pictus*. Anim. Conserv. 1, 1–9.

Crooks, K.R., Soule, M.E., 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400, 563–566.

Crowder, D.W., Snyder, W.E., 2010. Eating their way to the top? Mechanisms underlying the success of invasive insect generalist predators. Biol. Invasions 12, 2857–2876.

Darnell, A.M., Graf, J.A., Somers, M.J., Slotow, R., Gunther, M.S., 2014. Space use of African wild dogs in relation to other large carnivores. PLoS One 9.

Davis, N.E., Forsyth, D.M., Triggs, B., Pascoe, C., Benshemesh, J., Robley, A., Lawrence, J., Ritchie, E.G., Nimmo, D.G., Lumsden, L.F., 2015. Interspecific and geographic variation in the diets of sympatric carnivores: dingoes/wild dogs and red foxes in South-Eastern Australia. PLoS One 10, e0120975.

Denno, R.F., McClure, M.S., Ott, J.R., 1995. Interspecific interactions in phytophagous insects- competition reexamined and resurrected. Annu. Rev. Entomol. 40, 294–331.

Denno, R.F., Gratton, C., Peterson, M.A., Langellotto, G.A., Finke, D.L., Huberty, A.F., 2002. Bottom-up forces mediate natural-enemy impact in a phytophagous insect community. Ecology 83, 1443–1458.

Duffy, J.E., 2002. Biodiversity and ecosystem function: the consumer connection. Oikos 99, 201–219.

Duffy, J.E., Cardinale, B.J., France, K.E., McIntyre, P.B., Thebault, E., Loreau, M., 2005. The functional role of biodiversity in ecosystems: incorporating trophic complexity. Ecol. Lett. 10, 522–538.

Eldridge, S.R., Shakeshaft, B.J., Nano, T.J., 2002. The impact of wild dog control on cattle, native and introduced herbivores and introduced predators in central Australia. Final Report to the Bureau of Rural Sciences. Parks and Wildlife Commission of the Northern Territory, Alice Springs.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soule, M.E., Virtanen, R., Wardle, D.A., 2011. Trophic downgrading of planet Earth. Science 333, 301–306.

Eubanks, M.D., Denno, R.F., 1999. The ecological consequences of variation in plants and prey for an omnivorous insect. Ecology 80, 1253–1266.

Eubanks, M.D., Denno, R.F., 2000. Host plants mediate omnivore-herbivore interactions and influence prey suppression. Ecology 81, 936–947.

Fill, A., Long, E.Y., Finke, D.L., 2012. Non-consumptive effects of a natural enemy on a non-prey herbivore population. Ecol. Entomol. 37, 43–50.

Finke, D.L., Denno, R.F., 2002. Intraguild predation diminished in complex-structured vegetation: implications for prey suppression. Ecology 83, 643–652.

Finke, D.L., Denno, R.F., 2004. Predator diversity dampens trophic cascades. Nature 429, 407–410.

Finke, D.L., Denno, R.F., 2005. Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. Ecol. Lett. 8, 1299–1306.

Fleming, P.J.S., Allen, B.L., Ballard, G., 2012. Seven considerations about dingoes as biodiversity engineers: the socioecological niches of dogs in Australia. Aust. Mammal. 34, 119–131.

Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T., Mao, J.S., 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86, 1320–1330.

Gable, J.T., Crowder, D.W., Northfield, T.D., Steffan, S.A., Snyder, W.E., 2012. Niche engineering reveals complementary resource use. Ecology 93, 1994–2000.

Glen, A.S., 2012. Enough dogma: seeking the middle ground on the role of dingoes. Curr. Zool. 58, 856–858.

Glen, A.S., Dickman, C.R., Soule, M.E., Mackey, B.G., 2007. Evaluating the role of the dingo as a trophic regulator in Australian ecosystems. Austral Ecol. 32, 492–501.

Gordon, C.E., Feit, A., Gruber, J., Letnic, M., 2015. Mesopredator suppression by an apex predator alleviates the risk of predation perceived by small prey. Proc. R. Soc. B Biol. Sci. 282.

Gorman, M.L., Mills, M.G., Raath, J.P., Speakman, J.R., 1998. High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. Nature 391, 479–481.

Grez, A.A., Zaviezo, T., Gardiner, M.M., 2014. Local predator composition and landscape affects biological control in alfalfa fields. Biol. Control 76, 1–9.

Gunther, K.A., Smith, D.W., 2004. Interactions between wolves and female grizzly bears with cubs in Yellowstone National Park. Ursus 15, 232–238.

Hairston, N.G., Smith, F.E., Slobodkin, L.B., 1960. Community structure, population control, and competition. Am. Nat. 421–425.

Haswell, P.M., Kusak, J., Hayward, M.W., 2017. Large carnivore impacts are context-dependent. Food Webs 12, 3–13.

Hayes, R.D., Farnell, R., Ward, R.N.P., O'Donoghue, M., 2003. Experimental reduction of wolves in the Yukon: ungulate responses and management implications. Wildl. Monogr. 152, 1–35.

Hayward, M.W., Marlow, N., 2014. Will dingoes really conserve wildlife and can our methods tell? J. Appl. Ecol. 51, 835–838.

Hayward, M.W., Boitani, L., Burrows, N.D., Funston, P.J., Karanth, K.U., MacKenzie, D.I., Pollock, K.H., Yarnell, R.W., 2015. Ecologists need robust survey designs, sampling and analytical methods. J. Appl. Ecol. 52, 286–290.

Hervieux, D., Hebblewhite, M., Stepnisky, D., Bacon, M., Boutin, S., 2014. Managing wolves (*Canis lupus*) to recover threatened woodland caribou (*Rangifer tarandus caribou*) in Alberta. Can. J. Zool. 92, 1029–1037.

Holt, R.D., Lawton, J.H., 1994. The ecological consequences of shared natural enemies. Annu. Rev. Ecol. Evol. 25, 495–520.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol. Monogr. 75, 3–35.

Hurd, L.E., Eisenberg, R.M., 1984. Experimental density manipulations of the predator *Tenorera sirensis* (Orthoptera, Mantidae) in an old-field community.1. Mortality, development, and dispersal of juvenile mantids. J. Anim. Ecol. 53, 269–281.

Ives, A.R., Cardinale, B.J., Snyder, W.E., 2005. A synthesis of subdisciplines: predator-prey interactions, and biodiversity and ecosystem functioning. Ecol. Lett. 8, 102–116.

Johnson, C., 2006. Australia's Mammal Extinctions: A 50,000 Year History. Cambridge University Press, Melbourne.

Kauffman, M.J., Brodie, J.F., Jules, E.S., 2010. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade. Ecology 91, 2742–2755.

Kozar, F., Brown, M.W., Lightner, G., 1994. Spatial distribution of homopteran pests and beneficial insects in an orchard and its connection with ecological plant protection. J. Appl. Entomol. 117, 519–529.

Kruess, A., Tscharntke, T., 1994. Habitat fragmentation, species loss, and biological-control. Science 264, 1581–1584.

Kunkel, K.E., Ruth, T.K., Pletscher, D.H., Hornocker, M.G., 1999. Winter prey selection by wolves and cougars in and near Glacier National Park, Montana. J. Wildl. Manag. 63, 901–910.

Langellotto, G.A., Denno, R.F., 2004. Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. Oecologia 139, 1–10.

Laundre, J.W., Hernandez, L., Altendorf, K.B., 2001. Wolves, elk, and bison: reestablishing the "andscape of fear" in Yellowstone National Park, USA. Can. J. Zool. 79, 1401–1409.

Letnic, M., Crowther, M.S., Koch, F., 2009a. Does a top-predator provide an endangered rodent with refuge from an invasive mesopredator? Anim. Conserv. 12, 302–312.

Letnic, M., Koch, F., Gordon, C., Crowther, M.S., Dickman, C.R., 2009b. Keystone effects of an alien top-predator stem extinctions of native mammals. Proc. R. Soc. B Biol. Sci. 276, 3249–3256.

Letnic, M., Koch, F., 2010. Are dingoes a trophic regulator in arid Australia? A comparison of mammal communities on either side of the dingo fence. Austral Ecology 35, 167–175.

Letnic, M., Dworjanyn, S.A., 2011. Does a top predator reduce the predatory impact of an invasive mesopredator on an endangered rodent? Ecography 34, 827–835.

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

Letourneau, D.K., Jedlicka, J.A., Bothwell, S.G., Moreno, C.R., 2009. Effects of natural enemy biodiversity on the suppression of arthropod herbivores in terrestrial ecosystems. Annu. Rev. Ecol. Evol. Syst. 40, 573–592.

Marshall, K.N., Hobbs, N.T., Cooper, D.J., 2013. Stream hydrology limits recovery of riparian ecosystems after wolf reintroduction. Proc. R. Soc. B 280, 20122977.

McKenzie, N.L., Burbidge, A.A., Baynes, A., Brereton, R.N., Dickman, C.R., Gordon, G., Gibson, L.A., Menkhorst, P.W., Robinson, A.C., Williams, M.R., Woinarski, J.C.Z., 2007. Analysis of factors implicated in the recent decline of Australia's mammal fauna. J. Biogeogr. 34, 597–611.

McKnight, T.L., 1969. Barrier fencing for vermin control in Australia. Geogr. Rev. 59, 330–347.

Mech, L.D., 2012. Is science in danger of sanctifying the wolf? Biol. Conserv. 150, 143–149.

Middleton, A.D., Kauffman, M.J., McWhirter, D.E., Jimenez, M.D., Cook, R.C., Cook, J.G., Albeke, S.E., Sawyer, H., White, P.J., 2013. Linking anti-predator behaviour to prey demography reveals limited risk effects of an actively hunting large carnivore. Ecol. Lett. 16, 1023–1030.

Mills, M.G.L., Gorman, M.L., 1997. Factors affecting the density and distribution of wild dogs in the Kruger National Park. Conserv. Biol. 11, 1397–1406.

Mitchell, B.D., Banks, P.B., 2005. Do wild dogs exclude foxes? Evidence for competition from dietary and spatial overlaps. Austral Ecol. 30, 581–591.

Moran, M.D., Hurd, L.E., 1994. Short-term responses to elevated predator densities - noncompetitive intraguild interactions and behavior. Oecologia 98, 269–273.

Moran, M.D., Hurd, L.E., 1998. A trophic cascade in a diverse arthropod community caused by a generalist arthropod predator. Oecologia 113, 126–132.

Moran, M.D., Rooney, T.P., Hurd, L.E., 1996. Top-down cascade from a bitrophic predator in an old-field community. Ecology 77, 2219–2227.

Moseby, K.E., Neilly, H., Read, J.L., Crisp, H.A., 2012. Interactions between a top order predator and exotic mesopredators in the Australian rangelands. Int. J. Ecol. Article ID 250352 (15 pages).

Nelson, J.L., Cypher, B.L., Bjurlin, C.D., Creel, S., 2007. Effects of habitat on competition between kit foxes and coyotes. J. Wildl. Manag. 71, 1467–1475.

Newsome, A.E., Catling, P.C., Cooke, B.D., Smyth, R., 2001. Two ecological universes separated by the Dingo Barrier Fence in semi-arid Australia: interactions between landscapes, herbivory and carnivory, with and without dingoes. Rangel. J. 23, 71–98.

Newsome, T.M., Ballard, G.A., Crowther, M.S., Dellinger, J.A., Fleming, P.J.S., Glen, A.S., Greenville, A.C., Johnson, C.N., Letnic, M., Moseby, K.E., Nimmo, D.G., Nelson, M.P., Read, J.L., Ripple, W.J., Ritchie, E.G., Shores, C.R., Wallach, A.D., Wirsing, A.J., Dickman, C.R., 2015. Resolving the value of the dingo in ecological restoration. Restor. Ecol. 23, 201–208.

Nimmo, D.G., Watson, S.J., Forsyth, D.M., Bradshaw, C.J.A., 2015. Dingoes can help conserve wildlife and our methods can tell. J. Appl. Ecol. 52, 281–285.

Northfield, T.D., Snyder, G.B., Ives, A.R., Snyder, W.E., 2010. Niche saturation reveals resource partitoning among consumers. Ecol. Lett. 13, 338–348.

Pell, J.K., Baverstock, J., Roy, H.E., Ware, R.L., Majerus, M.E.N., 2008. Intraguild predation involving *Harmonia axyridis*: a review of current knowledge and future perspectives. Biocontrol 53, 147–168.

Philpott, S.M., Pardee, G.L., Gonthier, D.J., 2012. Cryptic biodiversity effects: importance of functional redundancy revealed through addition of food web complexity. Ecology 93, 992–1001.

Polis, G.A., 1991. Complex trophic interactions in deserts: an empirical critique of food web theory. Am. Nat. 138, 123–155.

Polis, G.A., Holt, R.D., 1992. Intraguild predation- the dynamics of complex trophic interactions. Trends Ecol. Evol. 7, 151–154.

Polis, G.A., Myers, C.A., Holt, R.D., 1989. The ecology and evolution of intraguild predation - potential competitors that eat each other. Annu. Rev. Ecol. Syst. 20, 297–330.

Pople, A.R., Grigg, G.C., Cairns, S.C., Beard, L.A., Alexander, P., 2000. Trends in the numbers of red kangaroos and emus on either side of the South Australian dingo fence: evidence for predator regulation? Wildl. Res. 27, 269–276.

Prasad, R.P., Snyder, W.E., 2006. Diverse trait-mediated interactions in a multi-predator, multi-prey community. Ecology 87, 1131–1137.

Preisser, E.L., Bolnick, D.I., Benard, M.F., 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. Ecology 86, 501–509.

Radloff, F.G.T., Toit, J.T.du, 2004. Large predators and their prey in a southern African savanna: a predator's size determines its prey size range. J. Appl. Ecol. 73, 410–423.

Ramirez, R.A., Rubanks, M.D., 2016. Herbivore density mediates the indirect effect of herbivoes on\ plants via induced resistance and apparent competition. Ecosphere 2, e01218.

Ripple, W.J., Beschta, R.L., 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? Bioscience 54, 755–766.

Ripple, W.J., Beschta, R.L., 2007. Restoring Yellowstone's aspen with wolves. Biol. Conserv. 138, 514–519.

Ripple, W.J., Larsen, E.J., 2000. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. Biol. Conserv. 95, 361–370.

Ripple, W.J., Larsen, E.J., Renkin, R.A., Smith, D.W., 2001. Trophic cascades among wolves, elk, and aspen in Yellowstone National Park's northern range. Biol. Conserv. 102, 227–234.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and ecological effects of the world's largest carnivores. Science 343, 151–163.

Ritchie, E.G., Johnson, C.N., 2009. Predator interactions, mesopredator release and biodiversity conservation. Ecol. Lett. 12, 982–998.

Ritchie, E.G., Elmhagen, B., Glen, A.S., Letnic, M., Ludwig, G., McDonald, R.A., 2012. Ecosystem restoration with teeth: what role for predators? Trends Ecol. Evol. 27, 265–271.

Romme, W.H., Turner, M.G., Wallace, L.L., Walker, J.S., 1995. Aspen, elk, and fire in northern Yellowstone-National-Park. Ecology 76, 2097–2106.

Rosenheim, J.A., Wilhoit, L.R., Armer, C.A., 1993. Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. Oecologia 96, 439–449.

Schmitz, O.J., 1998. Direct and indirect effects of predation and predation risk in old-field interaction webs. Am. Nat. 151, 327–342.

Schmitz, O.J., 2005. Scaling from plot experiments to landscapes: studying grasshoppers to inform forest ecosystem management. Oecologia 145, 225–234.

Schmitz, O.J., Beckerman, A.P., Obrien, K.M., 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. Ecology 78, 1388–1399.

Schmitz, O.J., Krivan, V., Ovadia, O., 2004. Trophic cascades: the primacy of trait-mediated interactions. Ecol. Lett. 7, 153–163.

Sergio, F., Schmitz, O.J., Krebs, C.J., Holt, R.D., Heithaus, M.R., Wirsing, A.J., Ripple, W.J., Ritchie, E., Ainley, D., Oro, D., Jhala, Y., Hiraldo, F., Korpimaki, E., 2014. Towards a cohesive, holistic view of top predation: a definition, synthesis and perspective. Oikos 123, 1234–1243.

Singer, F.J., Norland, J.E., 1994. Niche relationships within a guild of ungulate species in Yellowstone National Park, Wyoming, following release from artificial controls. Can. J. Zool. 72, 1383–1394.

Sitvarin, M.I., Rypstra, A.L., 2014. The importance of intraguild predation in predicting emergent multiple predator effects. Ecology 95, 2936–2945.

Smith, A.P., Quin, D.G., 1996. Patterns and causes of extinction and decline in Australian conilurine rodents. Biol. Conserv. 77, 243–267.

Snyder, W.E., Hurd, L.E., 1995. Egg-hatch phenology and intraguild predation between two mantid species. Oecologia 104, 496–500.

Snyder, W.E., Snyder, G.B., Finke, D.L., Straub, C.S., 2006. Predator biodiversity strengthens herbivore suppression. Ecology Letters 9, 789–796.

Snyder, W.E., Snyder, G.B., Finke, D.L., Straub, C.S., 2008. Predator biodiversity strengthens herbivore suppression. Ecol. Lett. 9, 789–796.

Steffen, S.A., Snyder, W.E., 2010. Cascading diversity effects transmitted exclusively by behavioral interactions. Ecology 91, 2242–2252.

Straub, C.S., Finke, D.L., Snyder, W.E., 2008. Are the conservation of natural enemy biodiversity and biological control compatible goals? Biol. Control 45, 225–237.

Straub, C.S., Snyder, W.E., 2006. Species identity dominates the relationship between predator biodiversity and herbivore suppression. Ecology 87, 277–282.

Swanson, A., Caro, T., Davies-Mostert, H., Mills, M.G.L., Macdonald, D.W., Borner, M., Masenga, E., Packer, C., 2014. Cheetahs and wild dogs show contrasting patterns of suppression by lions. J. Anim. Ecol. 83, 1418–1427.

Takizawa, T., Snyder, W.E., 2011a. Cannibalism and intraguild predation of eggs within a diverse predator assemblage. Environ. Entomol. 40, 8–14.

Takizawa, T., Snyder, W.E., 2011b. Predator biodiversity increases the survivorship of juvenile predators. Oecologia 166, 723–730.

Uriarte, M., Schmitz, O.J., 1998. Trophic control across a natural productivity gradient with sap-feeding herbivores. Oikos 82, 552–560.

Van Der Meer, E., Moyo, M., Rasmussen, G.S.A., Fritz, H., 2011. An empirical and experimental test of risk and costs of kleptoparasitism for African wild dogs (*Lycaon pictus*) inside and outside a protected area. Behav. Ecol. 22, 985–992.

Vanak, A.T., Fortin, D., Thaker, M., Ogden, M., Owen, C., Greatwood, S., Slotow, R., 2013. Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. Ecology 94, 2619–2631.

Wallach, A.D., Johnson, C.N., Ritchie, E.G., O'Neill, A.J., 2010. Predator control promotes invasive dominated ecological states. Ecol. Lett. 13, 1008–1018.

Wallach, A.D., Izhaki, I., Toms, J.D., Ripple, W.J., Shanas, U., 2015. What is an apex predator? Oikos 124, 1453–1461.

Werner, E.E., Peacor, S.D., 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology 84, 1083–1100.