Methods in Ecology and Evolution

Methods in Ecology and Evolution 2017, **8,** 135–142 doi: 10.1111/2041-210X.12663

Trophic cascades in 3D: network analysis reveals how apex predators structure ecosystems

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Summary

1. Trophic cascade theory predicts that apex predators structure ecosystems by regulating mesopredator and herbivore abundance and behaviour. Studies on trophic cascades have typically focused on short linear chains of species interactions. A framework that integrates more realistic and complex interactions is needed to make broader predictions on ecosystem structuring.

2. Network analysis is used to study food webs and other types of species interaction networks. These often comprise large numbers of species but rarely account for multiple interaction types and strengths. Here, we develop an intermediate complexity theoretical framework that allows specification of multiple interaction types and strengths for the study of trophic cascades. This ecological network is designed to suit data typically derived from field-based studies. The trophic cascade network contains fewer nodes than food webs, but provides semi-weighted directional links that enable different types of interactions to be included in a single model.

3. We use this trophic cascade network model to explore how an apex predator shapes ecosystem structure in an Australian arid ecosystem. We compared two networks that contrasted in the dominance of an apex predator, the dingo (*Canis dingo*), using published results ranking the direction and strength of key interactions. Nodes and links interacted dynamically to shape these networks. We examined how changes to an apex predator population affect ecosystem structure through their direct and indirect influences on different components of this ecological community.

4. Under strong apex predator influence, the network structure was denser and more complex, even and top-down driven; and dingo predation and soil commensalism formed denser interactive modules. Under weak apex predator influence (e.g. reflecting predator control), the resulting network structure was frayed, with mesopredator predation and grazing forming modules.

5. Our study demonstrates that networks of intermediate complexity can provide a powerful tool for elucidating potential ecosystem-wide effects of apex predators and predicting the consequences of management interventions such as predator control. Integrating trophic cascades, with their array of complex interactions, with the three-dimensional structure of ecological networks, has the potential to reveal 'ecological architecture' that neither captures on its own.

Key-words: bioturbation, dingo, ecosystem structure, food webs, mutualism, predation, top-down regulation

Introduction

The role of apex predators as ecosystem regulators is now firmly embedded in ecological theory, suggesting that the world is green and biologically diverse in large part because predators suppress herbivore densities (Hairston, Smith & Slobodkin 1960; Estes *et al.* 2011; Ripple *et al.* 2014). Studies from across the globe show that apex predators limit the abundance and modify the behaviour of their prey and smaller mesopredators, suppressing grazing and predation pressure, and enhancing biodiversity and productivity (Ritchie & Johnson 2009; Ritchie *et al.* 2012). This top-down forcing cascades throughout ecosystems influencing a broad range of processes, both biotic and abiotic, including species abundances and richness, animal behaviour, disease dynamics, carbon sequestration and stream morphology (Estes *et al.* 2011; Ripple *et al.* 2014; Atwood *et al.* 2015). The rise and fall of apex predators not only affects the composition of species

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*Correspondence author. E-mail: arian.wallach@uts.edu.au within ecological communities therefore, but also ecosystem functioning (Estes *et al.* 2011; Ripple *et al.* 2014; Standish *et al.* 2014). For example, wolves (*Canis lupus*) provide critical resource subsidies to scavenging species during warm months, thus enhancing their resilience to shortening winters due to global warming (Wilmers & Getz 2005). Similarly, dingoes (*C. dingo*) stabilize herbivore prey densities by dampening their population responses to rainfall in arid environments, thereby enabling plant biomass to accumulate during brief wet seasons (Letnic & Crowther 2013).

Trophic cascades are typically studied as relatively short and hierarchical chains of interactions, tested for relative strength and direction (e.g. predator $\rightarrow^{-}$ herbivore $\rightarrow^{-}$ vegetation) (Bascompte & Stouffer 2009; Ritchie & Johnson 2009). Trophic cascade theory, however, aims to explain much broader patterns in nature and is therefore well placed to be studied in an ecological network context (Montoya, Pimm & Sole 2006; Bascompte 2009). Ecological network analysis can be used to explore questions pertaining to community structure and dynamics, and to provide a platform for identifying features that maintain and enhance biodiversity (Montoya, Pimm & Sole 2006; Bascompte 2009; Thompson *et al.* 2012). For example, networks have been used to identify keystone species, elements and trophic structures that confer resistance to different types of perturbations, and to investigate the influence of adding or removing species from ecosystems (Montoya, Pimm & Sole 2006; Bascompte 2009; Säterberg, Sellman & Ebenman 2013). Furthermore, ecological networks provide a powerful tool for exploring the interconnectivity of nature and for predicting the robustness or fragility of ecosystem states (Montoya, Pimm & Sole 2006; Pascual & Dunne 2006). They constitute our main tool for understanding the relationship between diversity and stability in natural communities (Allesina & Tang 2012).

Ecological network studies have traditionally focused on feeding interactions and mutualisms (Ings *et al.* 2009; Kéfi *et al.* 2012), but trophic cascade studies often include other types of interactions (e.g. interspecific killing, risk effects and competition) that vary in their strength (Creel & Christianson 2008; Ritchie & Johnson 2009). Large predators often hunt a variety of species, but their population level effect is usually restricted to only some of their prey. For example, dingoes prey on a wide range of animals, from very small (<1 kg) to very large (>100 kg), but they primarily suppress populations of medium to large animals (Letnic, Ritchie & Dickman 2012). Thus, the indirect effect of a large predator on a prey species can be positive if it suppresses another predator that exerts a stronger predation force on that prey (Letnic, Ritchie & Dickman 2012). Network analyses of trophic cascade studies are therefore well suited to an intermediate complexity approach that incorporates the strength and type of trophic interactions derived from well-studied relationships.

Understanding the importance of predator loss (Ripple *et al.* 2014) and reestablishment (Chapron *et al.* 2014) is of widespread theoretical and management interest, due to its relevance for actions such as limiting and recovering wildlife populations (Wallach *et al.* 2010; Ritchie *et al.* 2012; Newsome *et al.* 2015). Integrating trophic cascades, with their array of complex interactions, with the three-dimensional structure of ecological networks, has the potential to reveal 'ecological architecture' that neither captures on its own. The first aim of our study was to develop a network analysis method suitable for trophic cascade field studies, which incorporates different types, and varying strengths, of interactions into a single model. Our second aim was to examine and demonstrate the types of insights that arise from networks on the ecological role of apex predators. To achieve this, we developed a network model of well-studied trophic interactions including both suppressive and commensal interactions. We constructed the ecological network from several highly interactive species of the Australian arid zone (Glen & Dickman 2005; Dickman *et al.* 2014) and examined how ecosystem structure may respond to a functionally dominant or weakened dingo population.

Australia's apex predator, the dingo, plays a keystone role in enhancing biodiversity by limiting herbivore prey (e.g. kangaroos, *Macropus* spp.) and mesopredators (e.g. red foxes, *Vulpes vulpes*) (Letnic, Ritchie & Dickman 2012). Widespread persecution of dingoes is now understood to be a leading cause of a series of mammal extinctions across the continent (Johnson 2006), many of which played key ecosystem functions (Fleming *et al.* 2014). Medium-sized (critical weight range) mammals (35–5500 g) in arid environments have been particularly vulnerable to predation by mesopredators (Johnson & Isaac 2009). Many of Australia's digging mammals fall within this critical weight range, and consequently their bioturbation (soil disturbance) effects have declined. This ecological function enhances soil properties, such as turnover, organic matter and water infiltration, which promotes plants and provides habitat for other organisms (Fleming *et al.* 2014). Thus, suppressive feeding interactions by dingoes can cascade to influence mutualisms driven by other species.

We investigated the top-down effects of the dingo on ecosystem structure and function by comparing two scenarios: in the first, the dingo population is intact, and in the second, the dingo population is suppressed. Our model system predicts that suppressing the ecological role of dingoes can provoke structural changes to ecosystems resulting in shifts between alternative ecosystem states.

Materials and methods

Ecological networks consist of ecosystem units (e.g. species) – represented as *nodes* – that are connected through ecological relationships (e.g. trophic) – represented as *links*. Both nodes and links can vary in their *weight*, where *node weights* can represent a species' population size, biomass or ecological effect, and *link weights* can represent the strength (e.g. effect size) and type (e.g. predation) of interactions. For clarity, throughout this paper, species and elements are capitalized when referred to as nodes in the network (e.g. 'dingo' refers to the species and 'Dingo' refers to the node).

NETWORK COMPONENTS

We constructed an ecological network comprising nine nodes (Table 1) chosen to represent well-studied highly interactive species and elements

Table 1. Elements used to construct the network

Functional role	Representative species/element
Apex predator	Dingo
Mesopredator	Fox
Mesopredator	Cat
Large herbivore	Kangaroo
Medium herbivore and ecological engineer (bioturbation agent)	Rabbit
Small mammal	Small mammal
Medium insectivore and ecological engineer (bioturbation agent)	Bilby
Primary productivity	Vegetation
Soil	Soil

of the Australian arid ecosystem (Glen & Dickman 2005; Dickman *et al.* 2014). We focused on the arid zone, which encompasses about 70% of the continent, because most extinctions and range contractions – and most trophic cascade studies – have occurred in this region (Johnson & Isaac 2009; Letnic, Ritchie & Dickman 2012). We incorporated both suppressive interactions – predation and herbivory – and mutualisms – bioturbation and the effects of plants on soil.

We chose the dingo to represent an apex predator and focused the network analysis on how changes to this one species trigger shifts in ecosystem structure. The red fox and wild cat (*Felis catus*) were included in the network to represent highly interactive mesopredators. Herbivores were represented by rabbits (*Oryctolagus cuniculus*) and kangaroos. The greater bilby (*Macrotis lagotis*) was chosen to represent a non-herbivorous digging mammal that is threatened by mesopredator predation. Bilbies, rabbits and small mammals were all included as ecosystem engineers through their bioturbation effects. Small mammals, vegetation and soil were included as functional groups and ecosystem properties.

Trophic cascade studies traditionally focus on small sets of interactions, and we brought three studies together to develop our model. Link weights between the Dingo, Fox, Cat, Kangaroo, Rabbit, Small mammal and Vegetation nodes were assigned from the results of generalized linear models and principle component analyses reported in a trophic cascade study by Wallach *et al.* (2010). The network was expanded to include two additional nodes: Bilby and Soil to illustrate how studies can be combined to provide predictive tools to assess how the recovery or extirpation of an apex predator can affect ecosystem functions. Link weights generated from the Dingo, Fox and Cats nodes to the Bilby node were assigned from the generalized linear model reported in Southgate *et al.* (2007), and the effects of mammalian bioturbation by Rabbit, Bilby and Small mammal nodes on Soil were ranked from measurements conducted by James, Eldridge & Hill (2009). All three studies were conducted in the arid zone and together, when unified into an ecological network, provided a predictive model of how the recovery or suppression of dingoes may affect ecosystem function.

INCORPORATING INTERACTION STRENGTHS INTO A NETWORK MODEL

We applied a set of rules to translate the results from the selected studies on interaction strengths into link weights on a discrete scale ranging from −3 to +3, to represent strongly suppressive to strongly mutualistic interactions (Table S1, Supporting Information). For example, Dingo→ Fox was assigned a link weight of −3, while the Dingo→ Cat link was only ranked −2, because the models in the focal study (Wallach *et al.* 2010) show a stronger (×4) suppressive effect of dingoes on foxes than on cats (Table S2). This qualitative method for inferring interaction strengths enables different types of interactions (e.g. predation and bioturbation) to be included in a single model.

To simplify the analysis, each interaction type was assigned a fixed negative or positive value. For example, herbivory was always assigned a negative link value even though it can also be mutualistic (e.g. herbivores also promote the growth and reproduction of plants). Links represented direct interactions between pairs of nodes (e.g. Dingo→ Kangaroo), while indirect interactions (e.g. trophic cascades, Dingo→ Vegetation) were calculated from the closest set of links between disconnected nodes. Links were assigned a single direction from the 'affecting' to 'affected' nodes (e.g. the influence of a predator on a prey was included, but not vice versa). The three studies yielded 20 paired interactions varying in weight and direction (Table 2).

MODELLING TROPHIC CASCADES AS A NETWORK

The set of nine nodes and their 20 paired links formed the network structure. These were used to model how changes to the apex predator node trigger changes to the network structure. Node weights were assigned discrete values ranging from 1 to 3, representing a species' or element's (weak to strong) interactive strength within the network. Two versions of the network were derived representing two ecological states (ES) based on the functional condition of the apex predator population. In ES1, the weight of the Dingo node was ranked high

Table 2. Maximum link weights assigned based on key literature assessing ecological interaction strengths. A nil interaction was assigned where no significant interaction was detected in the studies, even if such interactions do exist in nature. Node *A* is affecting Node *B* but not vice versa. For reference details, see Table S2. Cell colours vary from red to green highlighting the corresponding values ranging from −3 to +3

	B							
A	Fox	Cat	Kangaroo	Rabbit	Small mammals	Bilby	Vegetation	Soil
Dingo	−3	−2	−3	−2	−1	−1	0	0
Fox		−1	0	−1	−1	−3	0	0
Cat			0	−1	−2	−2	0	0
Kangaroo				0	0	0	−3	0
Rabbit					0	0	−3	+2
Small mammals						0	−1	+1
Bilby							0	+2
Vegetation								+3

Box 1. The dynamic relation between node weight and link weight

Node and link weights interact dynamically to shape the network following a set of ‘game rules’. The published studies determined the link weights when the node weights are maximal (Table 2). When the weight of node A is reduced, so is its effect in the network and its link weight is also reduced (Table I). This adjusted link weight then determines the node weight of B (Table II). The relation between node and link weights is illustrated in Fig. I.

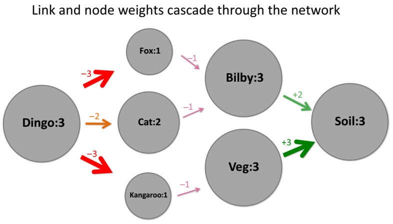
Table I. Maximum link weight ($A_{\max}\to^{X} B$) and the node weight of A ($A : X$) determine the adjusted link weight (A-X-B). As $A : X$ declines, link weight declines and in some cases the link severs

	$A_{\max}\to^{X} B$					
$A = X$	−3	−2	−1	1	2	3
$A = 3$	$A \to^{-3} B$	$A \to^{-2} B$	$A \to^{-1} B$	$A \to^{+1} B$	$A \to^{+2} B$	$A \to^{+3} B$
$A = 2$	$A \to^{-2} B$	$A \to^{-1} B$	/	/	$A \to^{+1} B$	$A \to^{+2} B$
$A = 1$	$A \to^{-1} B$	/	/	/	/	$A \to^{+1} B$

Table II. The adjusted link weight ($A \to^{X} B$) determines the node weight of B (B = X)

Link weight	Node weight
$A \to^{-3} B$	$B = 1$
$A \to^{-2} B$	$B = 2$
$A \to^{-1} B$	$B = 3$
$A \to^{+1} B$	$B = 1$
$A \to^{+2} B$	$B = 2$
$A \to^{+3} B$	$B = 3$

Fig. I. Illustration of how link and node weights cascade through the network.



(Dingo = 3), representing a condition in which the dingo population is present without restrictions. In ES2, the Dingo node weight was ranked low (Dingo = 1), to model a situation in which the apex predator is functionally absent or suppressed (e.g. subjected to lethal control). The effect of changing the weight of the Dingo node ‘cascaded’ throughout the network through a set of ‘game rules’ that determined the relationship between node and link weights (Box 1).

Let node A represents the affecting species/element (e.g. predator) and node B the affected species/element (e.g. prey) in each pair. The node weights are denoted as Node $A/B = X$, where $X = 1$, 2 or 3. The link weights are denoted $A \to^{X} B$, and the value of X ranges discretely from −3 to +3. The node weight of A combined with the link weight determined the node weight of B. The three key reference studies provided the maximum link weights when the node weight of A was maximal (denoted $A_{\max}$) (Table S2). If the node weight of A declined, so did its link weight and thus its overall effect in the network. The node weight of B was then determined by the adjusted link weight. For simplicity, the weight of node B was defined by the strongest interaction and was not cumulative.

Thus, suppressive interactions resulted in weaker nodes and weaker links, while mutualism interactions increased them. For example, a suppressive predator–prey interaction reduces the node weight of the prey and also the link weight generated by the prey. Thus, links between nodes that are connected via a trophic (feeding) interaction could be severed if the node weight and its associated link weight were sufficiently weakened. This represents interactions in nature in which feeding interactions do not result in discernible population level effects.

Assigning a maximal weight for the Dingo node (Dingo = 3) in ES1 and a minimal weight (Dingo = 1) in ES2, changed the node weights, adjusted the link weights and the number of links. Some links severed when the effect size became too low, leaving a total of 15 links in ES1 and 12 links in ES2 (Table S3).

NETWORK ANALYSIS

The adjusted node and link weights forming the two networks (Table S3) were analysed for four main properties: distance, quantitative degree, centrality and connectance.

Distance is a weighted measure of how close a given node is to another and represents its relative influence on it. Unlike link weights, this variable shows the influence of one node on another regardless of whether there are direct interactions between them. Distance is calculated using the units of link weights between pairs of nodes, and if the nodes are not linked, the distance used is calculated as the shortest path between them via other nodes (high link weights reduces the distance between nodes). We compared the average, standard deviation (SD) and coefficient of variance (CV) of distances, and identified modules of

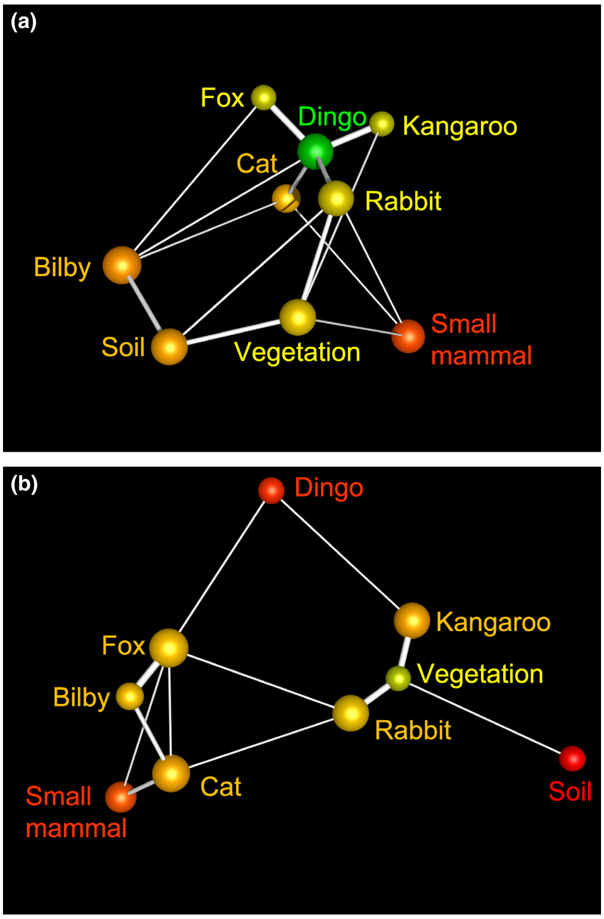


Fig. 1. Network structures of the two ecosystem states (ES) ES1 and ES2. In ES1, the Dingo node was assigned high weight score (a) and in ES2 a low weight score (b). The transition between the two states is shown in Video S1 (c). The volume of each ball indicates node weight, the thickness of lines represents link weight, and the length of lines denotes link distance. Colours range from red (low centrality score) to green (high centrality score). Centrality and link distance are scaled independently within each diagram.

higher density (lowest distances). We used a paired *t*-test (after verifying normal distribution, using a quantile–quantile plot) to compare distances between pairs of nodes in ES1 and ES2, and we identified modules (denser regions in the network) of node pairs with distances <1 and which differed by ×2 or more between ES1 and ES2.

Weighted degree represents the local importance of each node by its weighted connectivity within the network and is calculated by summing the absolute values of all the link weight values connected to that node. We compared the average (with a Paired *t*-test), SD and CV of node weights between the two networks.

Centrality is a measure that quantifies how close a given node is to every other node in the network. It is a measure commonly used to determine how important a node is globally based on its role as a connector between nodes. It is calculated as the average of the reciprocals of the network distances to each node as:

$$C_v(x) = \frac{1}{n-1}\left(\sum_{y\neq x}\frac{1}{d(x,y)}\right),$$

where $C_v(x)$ is the centrality of node x, n is the number of nodes in the network, and $d(x, y)$ is the network distance between nodes x and y (for directly linked nodes, this will simply be the reciprocal of the link

Table 3. Network structure of the two ecosystem states (ES) featuring the properties distance (a), degree (b) and centrality (c). Cells highlighted in green and blue have lower distances (>2) (a), and highest degree (b) and centrality (c) scores, for ES1 and ES2, respectively

(a)

Distance	ES1	ES2
Dingo–Fox	0·3	1
Dingo–Cat	0·5	1·8
Dingo–Kangaroo	0·3	1
Dingo–Rabbit	0·5	1·7
Dingo–Bilby	1	1·3
Dingo–Small mammal	1	2
Dingo–Vegetation	1	1·3
Dingo–Soil	1·5	2·3
Fox–Cat	0·8	0·8
Fox–Kangaroo	0·7	1·7
Fox–Rabbit	0·8	1
Fox–Bilby	1	0·3
Fox–Small mammal	1·3	1
Fox–Vegetation	1·3	1·3
Fox–Soil	1·5	2·3
Cat–Kangaroo	0·8	1·7
Cat–Rabbit	1	1
Cat–Bilby	1	0·5
Cat–Small mammal	1	0·5
Cat–Vegetation	1·5	1·3
Cat–Soil	1·5	2·3
Kangaroo–Rabbit	0·8	0·7
Kangaroo–Bilby	1·3	2
Kangaroo–Small mammal	1·3	2·2
Kangaroo–Vegetation	1	0·3
Kangaroo–Soil	1·5	1·3
Rabbit–Bilby	1·5	1·3
Rabbit–Small mammal	1·5	1·5
Rabbit–Vegetation	0·5	0·3
Rabbit–Soil	1	1·3
Bilby–Small mammal	2	1
Bilby–Vegetation	1	1·7
Bilby–Soil	0·5	2·7
Small mammal–Vegetation	1	1·8
Small mammal–Soil	1·5	2·8
Vegetation-Soil	0·5	1
Average	1·03	1·39
SD	0·41	0·66
CV (%)	39·39	47·78
Accumulated	37·2	50

(b)

Degree	ES1	ES2
Dingo	12	2
Fox	4	7
Cat	4	6
Kangaroo	4	4
Rabbit	5	5
Bilby	5	5
Small mammal	3	3
Vegetation	6	7
Soil	5	1
Average	5·3	4·4
SD	2·6	2·1
CV (%)	49·6	47·8
Accumulated	48	40

Table 3. (continued)

(c) Centrality	ES1	ES2
Dingo	1·71	0·7
Fox	1·26	1·12
Cat	1·09	1·07
Kangaroo	1·26	1·05
Rabbit	1·22	1·16
Bilby	0·99	1·12
Small mammal	0·79	0·82
Vegetation	1·18	1·3
Soil	1·04	0·56
Average	1·17	0·99
SD	0·25	0·24
CV (%)	21·57	24·42
Accumulated	10·5	8·9

weight). This definition of centrality, which differs from the more general usage (the reciprocal of the average distance), is more suitable for ecological network analysis because it remains well defined even if removal of a species results in disconnection of the network, causing some of the $d(x, y)$ to become infinite (Dekker 2005). We compared the average (with a paired t-test), SD and CV of centrality values between the two networks.

Connectance assesses the level of complexity of the network, by quantifying the density of interactions through the fraction of realized (out of the possible) links in the network:

$$C = \frac{L}{n} \times (n - 1),$$

where C is the network's connectance, L is the number of links, and n is the number of nodes (Pimm, Lawton & Cohen 1991).

Results

The node weights and adjusted link weights of ES1 and ES2 structured two distinct networks (Fig. 1). When the Dingo node weight was high (ES1), the network was denser, with 26% lower average distances between nodes, compared to the network in which the Dingo node was weakened (ES2) ($t = -3{\cdot}1$, d.f. = 35, $P < 0{\cdot}01$). ES1 was also more evenly shaped, with a lower CV of distances (Table 3a), and was more complex ($C = 0{\cdot}18$) than ES2 ($C = 0{\cdot}13$).

In the ES1 network, the Dingo was the most central and interconnected (degree score) node (Table 3b,c). In contrast, in ES2 the Vegetation and Fox nodes had the highest degree scores, and Vegetation was most central in the network (Table 3b,c). The average degree and centrality scores were 18–20% higher in ES1 compared to ES2, although these differences were not statistically significant. The degree and centrality scores of the Dingo and Soil nodes declined considerably when the Dingo node was weakened (Table 3b,c).

Distances between some node pairs differed substantially between ES1 and ES2 (Table 3a). In ES1, the Dingo node was at least three times closer to the Kangaroo, Fox, Cat and Rabbit nodes, and the Bilby node was over five times closer to Soil, compared to ES2. In ES2, the Fox node was three times closer to Bilby, and Kangaroo was three times closer to Vegetation, compared to ES1 (Table 3a).

These changes in distances formed internal modules of higher density (low distances). ES1 formed one module comprising of dingo predation interactions (Dingo–Cat/Fox/Kangaroo/Rabbit) and a second module of soil commensals (Vegetation/Bilby–Soil). ES2 formed a module of mesopredator predation (e.g. Fox/Cat–Bilby/Small mammal) and of grazing (Kangaroo–Vegetation) (Table 3a). In both ES1 and ES2, Fox–Cat/Rabbit and Rabbit–Vegetation remained similarly close.

Discussion

Network analysis can bring new insights into trophic cascade studies, complementing existing analysis tools. Using a network model of intermediate complexity, we showed how the direct effects of an apex predator on its prey influence fundamental network properties. We detected four main structural differences between the two modelled ecosystem states: density, complexity, evenness and top-down forcing. When the Dingo node was assigned a high score (ES1), the resulting network structure was denser, more even and complex and top-down forces dominated. By contrast, when the Dingo node was suppressed (ES2), the network structure was frayed and top-down forces were weakened. Our network analysis therefore suggests that the loss of apex predators leads to the 'unravelling' of ecosystems, consistent with theory (Estes *et al.* 2011).

In Australia, and globally, the decline of apex predators is often associated with increasing mesopredator predation and grazing pressure, which can shift ecosystems to alternative states (Wolf, Cooper & Hobbs 2007; Wallach *et al.* 2010; Ripple *et al.* 2014). Our network analysis revealed how changes in the status of the apex predator alter direct and indirect interactions between other species, forming contrasting ecosystem states. ES1 had modules around apex predator predation and soil mutualisms, and the Dingo node was highly interconnected and central. In contrast, ES2 had modules around mesopredator predation and grazing, the Vegetation and Fox nodes were the most interconnected, and Vegetation was central. Our model therefore predicts that increasing top-down forces by allowing dingoes to recover from lethal control is likely to benefit animals vulnerable to mesopredator predation (e.g. foxes→ bilbies) and promote their ecological function (e.g. bioturbation).

This suggests more broadly that top-down regulated ecosystems can be conducive to a range of mutualism interactions by other species. For example, beavers (*Castor canadensis*) drive mutualisms with other plants and animals by damming creeks. The eradication of wolves from Yellowstone National Park, North America, increased elk (*Cervus elaphus*) browsing to levels that excluded beavers, which shifted the stream habitat from ponds and floodplains – supporting structurally complex vegetation – to an alternative state that is channelled, eroded and surrounded by open grassland (Wolf, Cooper & Hobbs 2007). Similarly, predatory fish promote mutualisms between insect pollinators and plants, by feeding on the aquatic larval stage of predatory dragonfly (Knight *et al.* 2005). These cascades can be complex, however: wolves can also suppress beavers (Potvin *et al.* 1992; Rosell & Sanda 2006), and predators of mutualists can also have negative effects on plants (e.g. birds eating pollinating insects) (Knight *et al.* 2006).

We developed the current network from interaction strengths ranked according to single analyses, from a set of chosen studies, and it is likely that other data sets will yield differing results. The consistency of outcomes arising from network analyses is probably similar to that of other models, which are affected by natural and methodological variations between studies. Overall, we expect that our results are robust because the ecological effects of dingoes are typically consistent (Letnic, Ritchie & Dickman 2012). Studies conducted in deserts and forests have yielded strikingly similar results (Colman *et al.* 2014). Some variation between studies does exist, however. For example, we ranked the effect of dingoes on rabbits as quite strongly negative (following the results of Wallach *et al.* 2010), while other studies have reported positive interactions (Letnic, Ritchie & Dickman 2012).

A more comprehensive network analysis of trophic cascades would involve not only a larger number of nodes, but also dynamic bidirectional links. Here, for example, we focused on the top-down effect of the predator on the prey, excluding the bottom-up (resource) effects of prey on predators. These two-way interactions are important for investigating dynamic processes such as feedback loops (e.g. between plants and soil). Dynamic interactions also exist within species. For example, the mutualistic relationships within plant communities can trigger positive feedback loops that promote plant growth (McAlpine *et al.* 2009), and carnivore social behaviour can suppress population growth (Wallach *et al.* 2015). Future studies could also consider more nuanced interactions. We ranked trophic interactions as purely suppressive, even though herbivores also benefit plants, and we ranked animal–soil interactions as purely commensal, even though animals can also degrade soil.

Our study provides a proof of concept for the use of network analysis in the study of trophic cascades and highlights the benefits of adopting an intermediate complexity approach for analysis of field-based research. The approach extends trophic cascades from linear interactions, to system-level processes. The analysis demonstrates how networks could incorporate interactions that drive population dynamics, since not all feeding interactions drive populations. Mesoscale studies of ecological networks can reveal patterns in community assembly that are hard to study on large ecological networks and are not detectable at small (module) scales (Bascompte & Stouffer 2009). Finally, our study also provides a demonstration of how disparate field studies, with varying types of quantitative information, can be assembled into a network. For example, we extended a trophic cascade study (Wallach *et al.* 2010) by two nodes – Bilby and Soil (Southgate *et al.* 2007; James, Eldridge & Hill 2009) – to generate testable predictions on how the recovery of dingoes could increase mutualism interactions by a threatened ecosystem engineer [dingo$\rightarrow^{-}$ mesopredator$\rightarrow^{-}$ bilby$\rightarrow^{+}$ soil]. This is important because few studies are able to provide quantitative information on many nodes and links on their own.

Networks provide a helpful tool for integrating multiple interaction types within an ecosystem. They allow, for example, combining predator–prey interactions with ecosystem engineering (e.g. bioturbation) effects, as we have shown here. Such complexities constitute one of the biggest challenges in network ecology, affecting the structure, dynamics and functioning of communities (Ings *et al.* 2009; Kéfi *et al.* 2012). Our method (or an adaptation thereof) can be applied to the analysis of primary data sets, systematic reviews and theoretical studies, to help investigate 'big picture' questions and model scenarios that can be difficult to implement in the field.

Network-based ecological models can generate testable hypotheses on the consequences of adding and removing species from ecological communities and hence have important application for management actions such as enabling lethal control, enhancing protection and conducting reintroductions (Wallach *et al.* 2010; Ritchie *et al.* 2012; Ripple *et al.* 2014; Doherty *et al.* 2015). For example, the structural density of a network can predict the tendency of a given ecosystem to colonization, population increases and declines, and extinctions (Lurgi *et al.* 2014). Overall, the application of network analysis is a powerful way to conceptualize nature not only by its species, but also by the architecture of its interactions.

Acknowledgements

We thank the reviewers for helpful comments.

Data accessibility

This manuscript does not include any data.

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Received 14 June 2016; accepted 12 September 2016
Handling Editor: Diana Fisher

Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

Table S1. Method for assigning link weights from the results of measured species interactions.

Table S2. Description of studies used to assign link weight.

Table S3. Adjusted node and link weights entered into the network model.

Video S1. File for Fig. 1c (online viewing only): Transition between the network structures of two ecosystem states (ES) ES1 and ES2.