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

3

4 Running head: Trophic cascades in ecological networks

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6

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9

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20

21

22

23 **Abstract**

24 1. Trophic cascade theory predicts that apex predators structure ecosystems by
25 regulating mesopredator and herbivore abundance. Studies on trophic
26 cascades have typically focused on short linear chains of species
27 interactions. A framework that integrates more realistic and complex food
28 webs and interactions is needed if we are to make wider ecosystem scale
29 predictions on ecosystem structuring.

30

31 2. Network analysis has been successfully used to study food webs and other
32 types of species interaction networks. These often comprise large numbers
33 of species but rarely account for multiple interaction types, and do not
34 always contain information on interaction strengths. Here we develop an
35 intermediate complexity theoretical framework that allows specification of
36 multiple interaction types and strengths for the study of trophic cascades in
37 an ecological network context. This framework is designed to suit data
38 typically derived from field-based studies of trophic cascades. The trophic
39 cascade network contains fewer nodes than food webs, but provides semi-
40 weighted directional links that enable different types of interactions,
41 including both feeding and non-feeding interactions, to be included in a
42 single model.

43

44 3. We employ this trophic cascade network model to explore how an apex
45 predator shapes ecosystem structural properties in a typical Australian arid
46 ecosystem. We compared two networks that contrasted in the dominance
47 of an apex predator, the dingo (*Canis dingo*), using published results

48 ranking the nature, direction and strength of key interactions. Nodes and
49 links interacted dynamically to shape these networks. We aim at revealing
50 the role of trophic cascades in structuring ecosystem through their direct
51 and indirect influences on different components of this ecological
52 community.

53

54 4. Under strong apex predator influence, the network structure was denser
55 and more complex, even, and top-down driven; and dingo predation and
56 soil commensalism formed denser interactive modules. Under weak apex
57 predator influence (e.g. reflecting a predator control scenario) the resulting
58 network structure was frayed, with mesopredator predation and grazing
59 forming prominent clusters. Our study demonstrates that networks of
60 intermediate complexity can provide a powerful tool for elucidating the
61 ecosystem-wide effects of apex predators, and its applicability to
62 predicting the consequences of management interventions such as predator
63 control.

64

65 **Key-words** Bioturbation, Dingo, Ecosystem structure, Food webs, Predator control,
66 Species interactions, Top-down regulation

67

68 **Introduction**

69 The role of apex predators as ecosystem regulators is now firmly embedded in
70 ecological theory, suggesting that the world is green and biologically diverse in large
71 part because predators suppress herbivore densities (Hairston, Smith & Slobodkin
72 1960; Estes *et al.* 2011; Ripple *et al.* 2014). Studies from across the globe show that

73 apex predators limit the abundance and modify the behaviour of their prey and smaller
74 mesopredators, suppressing grazing and predation pressure, and enhancing biodiversity
75 and productivity (Ritchie & Johnson 2009; Ritchie *et al.* 2012). This top-down forcing
76 cascades throughout ecosystems influencing a broad range of processes, both biotic and
77 abiotic, including species abundances and richness, animal behaviour, disease
78 dynamics, carbon sequestration and stream morphology (Estes *et al.* 2011; Ripple *et al.*
79 2014; Atwood *et al.* 2015). The rise and fall of apex predators not only affects the
80 composition of species within ecological communities therefore, but also ecosystem
81 functioning (Estes *et al.* 2011; Ripple *et al.* 2014; Standish *et al.* 2014). For example,
82 wolves (*Canis lupus*) provide critical resource subsidies to scavenging species during
83 warm months, thus enhancing their resilience to shortening winters due to global
84 warming (Wilmers & Getz 2005). Similarly, dingoes (*Canis dingo*) stabilize herbivore
85 prey densities by dampening their population responses to rainfall in arid environments,
86 thereby enabling plant biomass to accumulate during wet seasons (Letnic & Crowther
87 2013).

88

89 Trophic cascades are typically studied as relatively short and hierarchical chains of
90 interactions, tested for relative strength and direction, (e.g. predator [-] → herbivore [-]
91] → vegetation) (Bascompte & Stouffer 2009; Ritchie & Johnson 2009). Trophic
92 cascade theory however aims to explain much broader patterns in nature, and is
93 therefore well-placed to be studied in an ecological network context (Montoya, Pimm
94 & Sole 2006; Bascompte 2009). Ecological network analysis can be used to explore
95 questions pertaining to community structure and dynamics, and to provide a platform
96 for identifying features that maintain and enhance biodiversity (Montoya, Pimm & Sole
97 2006; Bascompte 2009; McCann 2011; Thompson *et al.* 2012). For example, networks

98 have been used to identify keystone species, elements and trophic structures that confer
99 resistance to different types of perturbations, and to investigate the influence of adding
100 or removing species from ecosystems (Dunne, Williams & Martinez 2002; Montoya,
101 Pimm & Sole 2006; Bascompte 2009; Säterberg, Sellman & Ebenman 2013; Lurgi *et*
102 *al.* 2014). Furthermore, ecological networks provide a powerful tool for exploring the
103 interconnectivity of nature and for predicting the robustness or fragility of ecosystem
104 states (Montoya, Pimm & Sole 2006; Pascual & Dunne 2006). They constitute our main
105 tool for understanding the relationship between diversity and stability in natural
106 communities (May 1972; McCann 2000; Allesina & Tang 2012).

107

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

121

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

138 Australia’s apex predator, the dingo, plays a keystone role in enhancing biodiversity by
139 limiting herbivore prey (e.g. kangaroos, *Macropus* spp.) and mesopredators (e.g. red
140 foxes, *Vulpes vulpes*) (Letnic, Ritchie & Dickman 2012). Widespread persecution of
141 dingoes is now understood to be a leading cause of a series of mammal extinctions
142 across the continent (Johnson 2006), many of which played key ecosystem functions
143 (Fleming et al. 2014). Medium-sized (critical weight range) mammals (35–5500 g) in
144 arid environments have been particularly vulnerable to predation by mesopredators
145 (Johnson & Isaac 2009). Many of Australia’s digging mammals fall within this critical
146 weight range, and consequently their bioturbation (soil disturbance) effects have

147 declined. This ecological function enhances soil properties, such as turnover, organic
148 matter and water infiltration, which promotes plants and provides habitat for other
149 organisms (Fleming et al. 2014). Thus, suppressive feeding interactions by dingoes can
150 cascade to influence mutualisms driven by other species.

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

156

157 **Materials and methods**

158 Ecological networks consist of ecosystem units (e.g. species) – represented as *nodes* –
159 that are connected through ecological relationships (e.g. trophic) – represented as *links*.
160 Both nodes and links can vary in their *weight*, where *node weights* can represent a
161 species' population size, biomass or ecological effect, and *link weights* can represent
162 the strength (e.g. effect size) and type (e.g. predation) of interactions. We define a
163 network of ecological interactions among entities in an Australian arid system in this
164 way. For clarity, throughout this paper, species and elements are capitalised when
165 referred to as nodes in the network (e.g. 'dingo' refers to the species and 'Dingo' refers
166 to the node).

167

168 **Network components**

169 We constructed an ecological network comprising nine nodes (Table 1) chosen to
170 represent well studied highly interactive species and elements of the Australian arid

171 ecosystem (Glen & Dickman 2005). We focused on the arid zone, which encompasses
172 about 70% of the continent, because most extinctions and range contractions – and most
173 trophic cascades studies – have occurred in this region (Johnson & Isaac 2009; Letnic,
174 Ritchie & Dickman 2012). We incorporated both suppressive interactions – predator-
175 prey and herbivory – and mutualistic interactions – bioturbation and the effects of plants
176 on soil.

177

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

188

189 Trophic cascades studies traditionally focus on small sets of interactions, and we
190 brought three studies together to define our model. Link weights between the Dingo,
191 Fox, Cat, Kangaroo, Rabbit, Small mammal and Vegetation nodes were assigned from
192 the results of generalised linear models and principle component analyses reported in a
193 trophic cascades study by Wallach *et al.* (2010). The network was expanded to include
194 two additional nodes: Bilby and Soil to illustrate how studies can be combined to
195 provide predictive tools to assess how the recovery or extirpation of an apex predator

196 can affect ecosystem functions. Link weights generated from the Dingo, Fox and Cats
197 nodes to the Bilby node were assigned from the generalised linear model reported in
198 Southgate *et al.* (2007), and the effects of mammalian bioturbation by Rabbit, Bilby
199 and Small mammal nodes on Soil were ranked from measurements conducted by James,
200 Eldridge and Hill (2009). All three studies were conducted in the arid zone and together,
201 when unified into a ecological network framework, provided a predictive model of how
202 the recovery or suppression of dingoes may affect ecosystem function.

203

204 **Incorporating interaction strengths into a network model**

205 We applied a set of rules to translate the results from the studies summarised above on
206 interaction strengths into link weights on a discrete scale ranging from -3 to +3, to
207 represent strongly suppressive to strongly commensal interactions (Table S1). For
208 example, Dingo→Fox was assigned a link weight of -3 while the Dingo→Cat link was
209 only ranked -2, because the models in the focal study (Wallach *et al.* 2010) show a
210 stronger (x4) suppressive effect of dingoes on foxes than on cats (Table S2). This
211 qualitative method for inferring interaction strengths enables different types of
212 interactions (e.g. predation and bioturbation) to be included in a single model.

213

214 To simplify the analysis, each interaction type was assigned a fixed negative or positive
215 value. For example, herbivory was always assigned a negative link value even though
216 it can also be commensal (e.g. herbivores also promote the growth and reproduction of
217 some plants). Links represented direct interactions between pairs of nodes (e.g.
218 Dingo→Kangaroo), while indirect interactions (e.g. trophic cascades, Dingo--
219 >Vegetation) were calculated from the closest set of links between disconnected nodes.
220 Links were assigned a single direction from the 'affecting' to 'affected' nodes (e.g. the

221 influence of a predator on a prey was included, but not vice versa). The three studies
222 yielded 20 paired-interactions varying in weight and direction (Table 2).

223

224 **Modelling trophic cascades as a network**

225 The set of nine nodes and their 20 paired links formed the network structure. There
226 were used to model how changes to the apex predator node trigger changes to the
227 network structure. Node weights were assigned discrete values ranging from 1 to 3,
228 representing weak to strong interactive strength within the network. Two versions of
229 the network were derived representing two ecological states (ES) based on the
230 functional condition of the apex predator population. In ES1, the weight of the dingo-
231 node was ranked high (Dingo=3), representing a condition in which the dingo is present
232 without restrictions. In ES2, the Dingo node weight was ranked low (Dingo=1), to
233 model a situation in which the apex predator is functionally absent or suppressed (e.g.
234 subjected to lethal control). The effect of changing the weight of the Dingo node
235 ‘cascaded’ throughout the network through a set of ‘game rules’ that determined the
236 relationship between node and link weights (Box 1).

237

238 Let node A represent the affecting species/element (e.g. predator) and node B the
239 affected species/element (e.g. prey) in each pair. The node weights are denoted as Node
240 A/B = X, where X = 1, 2 or 3. The link weights are denoted $A \rightarrow^X B$, and the value of
241 X ranges discretely from -3 to +3. The node weight of A combined with the link weight
242 determined the node weight of B. The three key reference studies provided the
243 maximum link weights when the node weight of A was maximal (denoted A_{\max}) (Table
244 S2). If the node weight of A declined, so did its link weight, and thus its overall effect
245 in the network. The node weight of B was then determined by the adjusted link weight.

246 For simplicity, the weight of node B was defined by the strongest interaction, and was
247 not cumulative.

248

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

256

257 **Network analysis**

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

260

261 *Distance* is a weighted measure of how close a given node is to another and represents
262 its relative influence on it. Unlike link weights, this variable shows the influence of one
263 node on another regardless of whether there are direct interactions between them.
264 Distance is calculated using the units of link weights between pairs of nodes, and if the
265 nodes are not linked, the distance used is calculated as the shortest path between them
266 via other nodes (high link weights reduces the distance between nodes). We compared
267 the average, standard deviation (SD) and coefficient of variance (CV) of distances, and
268 identified modules of higher density (lowest distance). We used a paired *t-test* (after
269 verifying normal distribution, using a quantile-quantile plot) to compare distances
270 between pairs of nodes in ES1 and ES2, and we identified modules (denser regions in

271 the network) of node pairs with distances <1 and which differed by x2 or more between
272 ES1 and ES2.

273

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

278

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

$$283 \quad C_V(x) = \frac{1}{n-1} \left(\sum_{y \neq x} \frac{1}{d(x,y)} \right)$$

284 where $C_V(x)$ is the centrality of node x , n is the number of nodes in the network, and
285 $d(x, y)$ is the network distance between nodes x and y (for directly linked nodes, this
286 will simply be the reciprocal of the link weight). This definition of centrality, which
287 differs from the more general usage (the reciprocal of the average distance), is more
288 suitable for ecological network analysis because it remains well-defined even if
289 removal of a species results in disconnection of the network, causing some of the $d(x,$
290 $y)$ to become infinite (Dekker 2005). We compared the average (with a paired *t-test*),
291 SD and CV of centrality values between the two networks.

292

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

295 $C = L / N \times (N-1)$

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

298

299 **Results**

300 The node weights and adjusted link weights of ES1 and ES2 structured two distinct
301 networks (Fig. 1). When the Dingo node weight was high (ES1) the network was
302 denser, with lower average distances between nodes (26%), and higher average degree
303 (17%) and centrality (15%) scores. ES1 was also more evenly shaped, with a lower
304 coefficient of variance (CV) of distances (Table 3a). ES1 was more complex ($C = 0.18$)
305 than ES2, where the Dingo node was weakened ($C = 0.13$).

306

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

314 Distances between some node pairs differed substantially between ES1 and ES2 (Table
315 3a). In ES1, the Dingo node was at least three times closer to the Kangaroo, Fox, Cat
316 and Rabbit nodes, and the Bilby node was over five times closer to Soil, compared to
317 ES2. In ES2, the Fox node was three times closer to Bilby, and Kangaroo was three
318 times closer to Vegetation, compared to ES1 (Table 3a).

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

325

326 **Discussion**

327 Network analysis can bring new insights into trophic cascade studies, complementing
328 existing analysis tools. We showed how the influence of an apex predator percolates
329 through an ecological network beyond trophic cascades via its indirect effects on other
330 components of the ecosystem it is embedded in. We investigated these effects using a
331 network model of intermediate complexity in interactions between entities were
332 determined from empirical data on the influence of each on one another. In our model
333 system, the direct effects of the apex predator on its prey influenced fundamental
334 network properties. We detected four main structural differences between the two
335 modelled ecosystem states: density, complexity, evenness and top-down forcing. When
336 the Dingo node was assigned a high score (ES1), the resulting network structure was
337 denser, more even and complex and top-down forces dominated. By contrast, when the
338 Dingo node was suppressed (ES2), the network structure was frayed and top-down
339 forces were weakened, evident by the centrality of the Vegetation and Fox nodes
340 (Wallach *et al.* 2010). Our network analysis therefore suggests that the loss of apex
341 predators leads to the ‘unravelling’ of ecosystems, consistent with theory (Estes *et al.*
342 2011).

343

344 In Australia, and globally, the decline of apex predators is often associated with
345 increasing mesopredator predation and grazing pressure, which can shift ecosystems to
346 alternative states (Wolf, Cooper & Hobbs 2007; Wallach *et al.* 2010; Ripple *et al.*
347 2014). Our network analysis revealed how changes in the status of the apex predator
348 alter direct and indirect interactions between other species, forming contrasting
349 ecosystem states. ES1 had modules around apex predator predation and soil
350 mutualisms, and the Dingo node was highly interconnected and central. In contrast, ES2
351 had modules around mesopredator predation and grazing, the Vegetation and Fox nodes
352 were the most interconnected, and Vegetation was central. Our model therefore predicts
353 that increasing top-down forces by allowing dingoes to recover from lethal control is
354 likely to benefit animals vulnerable to mesopredator predation (e.g. foxes → bilbies)
355 and promote their ecological function (e.g. bioturbation).

356

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

368 can also have negative effects on plants (e.g. birds eating pollinating insects) (Knight
369 *et al.* 2006).

370

371 We developed the current network from interaction strengths ranked according to single
372 analyses, from a set of chosen studies, and it is likely that other datasets will yield
373 differing results. The consistency of outcomes arising from network analyses is
374 probably similar to that of other models. We expect that our results are robust because
375 the ecological effects of dingoes has been demonstrably consistent (Letnic, Ritchie &
376 Dickman 2012). Studies conducted in deserts and forests have yielded strikingly similar
377 results (Colman *et al.* 2014). Some variation between studies does exist however. For
378 example, we ranked the effect of dingoes on rabbits as quite strongly negative
379 (following the results of Wallach *et al.* 2010), while other studies have found positive
380 interactions (Letnic, Ritchie & Dickman 2012).

381

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

392 though herbivores also benefit plants, and we ranked animal-soil interactions as purely
393 commensal, even though animals can also degrade soil.

394

395 Our study provides a proof of concept for the use of network analysis in the study of
396 trophic cascades and highlights the benefits of adopting an intermediate complexity
397 approach for analysis of field-based research. The approach extends trophic cascades
398 from linear interactions, to system-level processes. The analysis demonstrates how
399 networks could incorporate interactions that drive population dynamics, since not all
400 feeding-interactions drive populations. It has been argued that mesoscale studies of
401 ecological networks can reveal patterns in community assembly and disassembly that
402 are hard to study on large ecological networks and are not detectable at small (module)
403 scales (Bascompte & Stouffer 2009). Taking a mesocale approach to ecological
404 networks we show how trophic cascades can structure ecological communities and
405 affect their components in different ways. Finally, our study also provides a
406 demonstration of how disparate field studies, with varying types of quantitative
407 information, can be assembled into a network. For example, we extended a trophic
408 cascades study (Wallach et al. 2010) by two nodes (Bilby and Soil) to generate testable
409 predictions on how the recovery of dingoes could increase mutualism interactions by a
410 threatened ecosystem engineer [dingo(-)→ mesopredator(-)→ bilby(+)-> soil]. This is
411 important because few studies are able to provide quantitative information on many
412 nodes and links on their own.

413

414 Networks provide a helpful tool for integrating multiple interaction types within an
415 ecosystem. They allow for example, combining predator-prey interactions with
416 ecosystem engineering (e.g. bioturbation) effects as we have shown here. Such

417 complexities constitute one of the biggest challenges in network ecology, affecting the
418 structure, dynamics and functioning of communities (Ings *et al.* 2009; Kefi *et al.* 2012).
419 Our method (or an adaptation thereof) can be applied to the analysis of primary datasets,
420 systematic reviews and theoretical studies, to help investigate ‘big picture’ questions
421 and model scenarios that can be difficult to implement in the field.

422

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

432

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435

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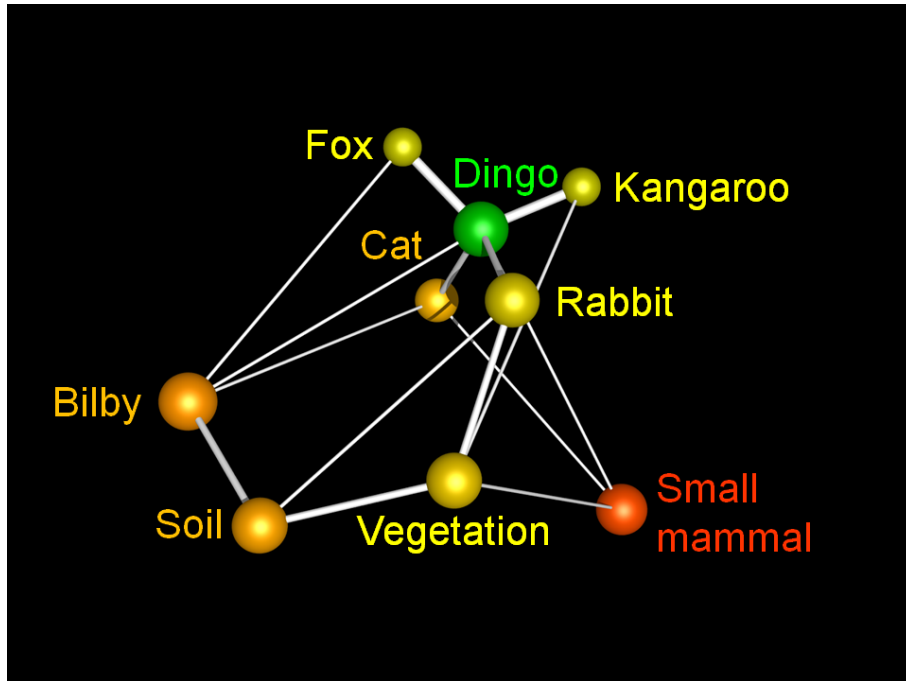
565 **Figures**

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567 **Fig. 1**

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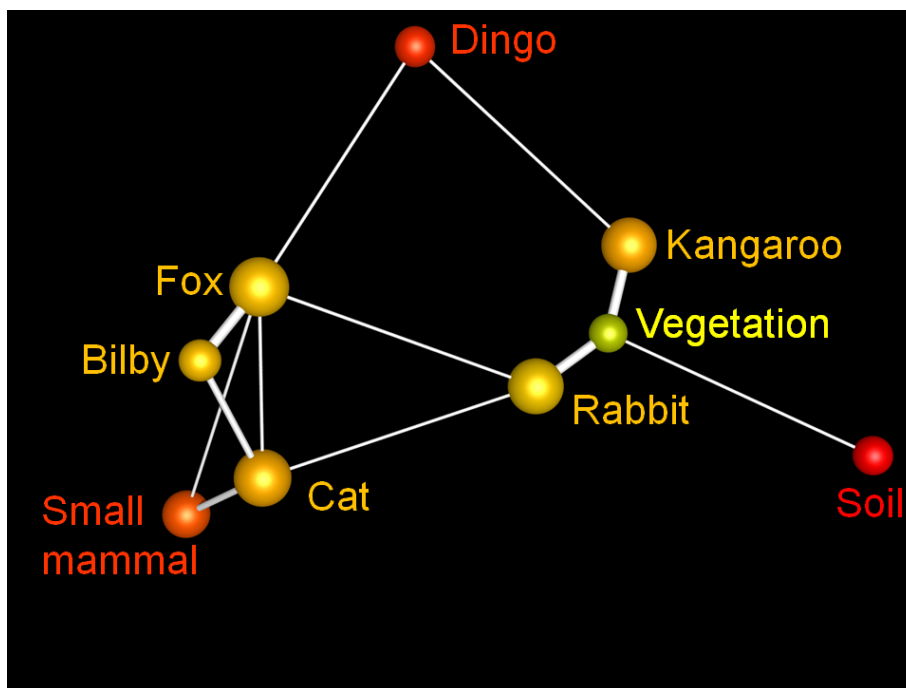
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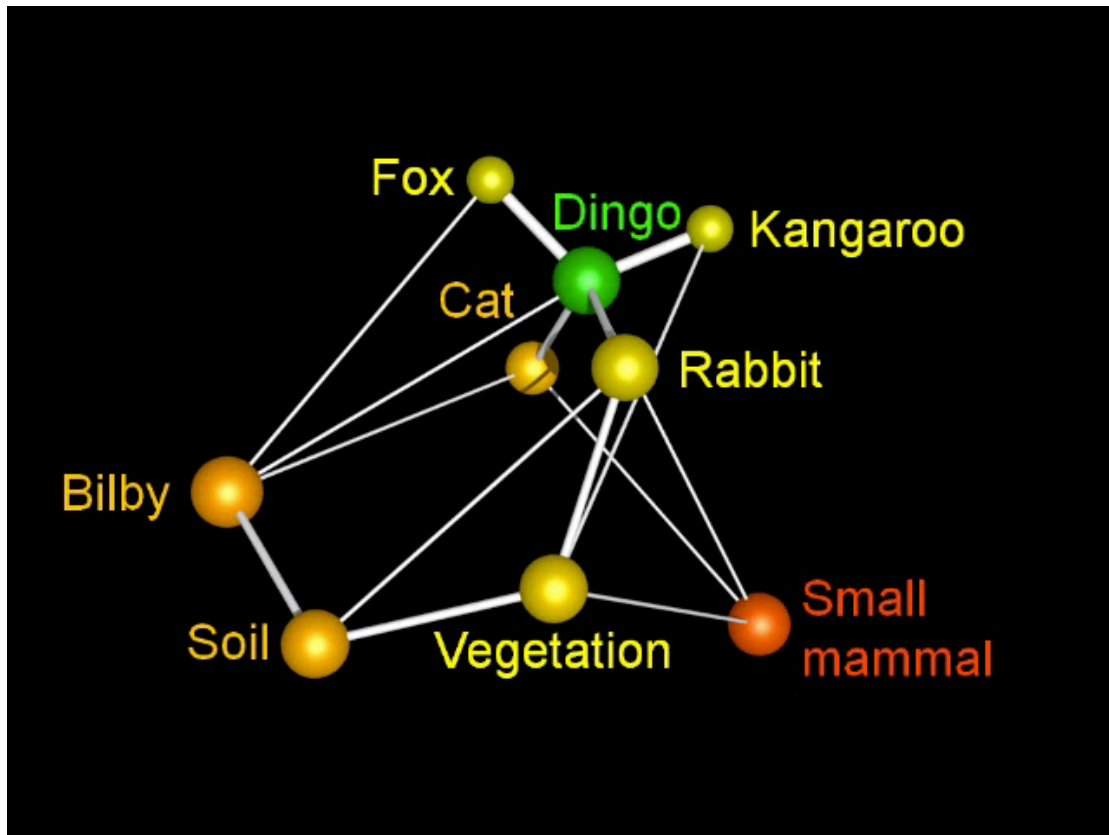
572 (b)



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

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587 **Tables**

588

589 **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

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592 **Table 2: Maximum link weights (i.e., ecological interactions strengths) assigned based on key literature**
 593 where no significant interaction was detected in the included studies, even if such interactions do exist in nature
 594 not vice versa (for reference details see Supplementary Material Table S2).

A \ B	Fox	Cat	Kangaroo	Rabbit	Small mammals	Bilby
Dingo	-3	-2	-3	-2	-1	-1
Fox		-1	0	-1	-1	-3
Cat			0	-1	-2	-2
Kangaroo				0	0	0
Rabbit					0	0
Small mammals						0
Bilby						
Vegetation						

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597 **Table 3: Network structure of the two ecosystem states (ES) featuring the**

598 **properties distance (a), degree (b) and centrality (c).** In (a) link distances that differ

599 by an order of two or more are highlighted with coloured cells (red cells are closer

600 and green cells are further). In (b) and (c) the nodes with the highest degrees and

601 centrality scores are highlighted in bold.

(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

(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

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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).

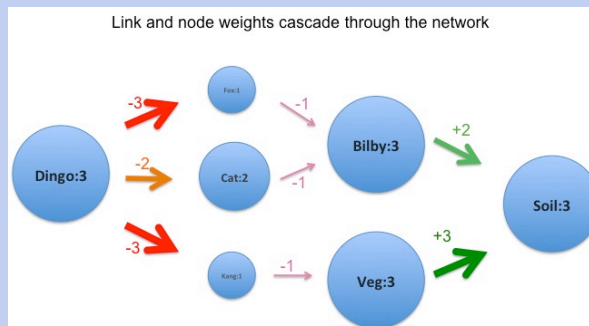


Table I - Maximum link weight ($A_{max} \rightarrow^X B$) and the node weight of A ($A:X$) determine the adjusted link weight ($A \rightarrow^X B$). As $A:X$ declines, link weight declines and in some cases the link severs.

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

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

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

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607 **Supporting Information**

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

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Interactions (A→B)	Link sign	Link weight assigned to species interaction if model result are:			Comments
		1	2	3	
Predation, interguild predation, and herbivory	-	Weakly negative to positive	Negative to weakly positive	Consistently negative	Predation and herbivory even if model results show bottom-up or indirect effects commensalism in these cases promote plant growth through and pruning).
Bioturbation (animal on soil)	+	Effect reported	Significant effect measured	(N/A)	Bioturbation was the only was considered purely to reduce quality (e.g. by causing was assigned a maximum effect than that exerted by
Vegetation on soil	+	(N/A)	(N/A)	Positive	Vegetation was assigned acknowledge the negative promoting fire).

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

Species A	Species B	Type of interactions	Study results	M
Study 1: Wallach et al. (2010)*				
Dingo	Fox	Interguild predation	Foxes are strongly and negatively associated with dingoes.	
Dingo	Cat	Interguild predation	Cats are negatively associated with dingoes.	
Dingo	Kangaroo	Predation	Kangaroos are strongly and negatively associated with dingoes.	
Dingo	Rabbit	Predation	Rabbits are negatively associated with dingoes.	
Dingo	Small mammals	Predation	Small mammals are positively associated with dingoes.	
Fox	Rabbit	Predation	Rabbit and fox densities are positively associated.	
Fox	Small mammals	Predation	Small mammal density is negatively associated with foxes in some models.	
Fox	Cat	Interguild predation	Cats and foxes are positively associated in all models.	
Cat	Rabbit	Predation	Rabbits are positively associated with cats in most models.	
Cat	Small mammals	Predation	Small mammals are negatively associated with cats.	

Kangaroo	Vegetation	Herbivory	Vegetation cover and diversity is negatively associated with kangaroo density.
Rabbit	Vegetation	Herbivory	Vegetation cover and diversity is negatively associated with rabbit density.
Small mammal	Vegetation	Herbivory	Vegetation cover and diversity is positively associated with small mammal density.

Study 2: Southgate et al. (2007)[†]

Dingo	Bilby	Predation	Model predicts that bilbies are strongly positively associated with dingo presence.
Fox	Bilby	Predation	Model predicts that bilby occurrence is strongly negatively related with foxes.
Cat	Bilby	Predation	Cats were a weak predictor of bilby persistence but can drive population declines.

Study 3: James et al. (2009)[‡]

Bilby	Soil	Bioturbation	Bilbies dig pits and turn over large quantities of soil trapping seeds and other plant debris.
Rabbit	Soil	Bioturbation	Rabbits dig pits and turn over large quantities of soil trapping seeds and other plant debris. This effect is weaker than the bilby but evidence stronger than for small mammals.
Small mammal	Soil	Bioturbation	Small mammals dig pits and burrows.

Vegetation	Soil	Nutrient and water retention	Vegetation promotes soil nutrient content, moisture and structural and temperature stability.
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* Results of generalised linear models (GLM) and the first two strongest Principle Component (PC) models and dashed lines denote that the variables were not included or were insignificant in the model, respectively.
† Generalised linear models (GLM) of predictor variables of bilby occurrence.
‡ Measurement of plant debris captured in pits constructed by ecological engineers.

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

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ES1 - Apex predator is dominant

ES2 - Apex predator is weakened

- **Dingo = 3**
- Dingo \rightarrow^{-3} Fox
- Dingo \rightarrow^{-2} Cat
- Dingo \rightarrow^{-3} Kangaroo
- Dingo \rightarrow^{-2} Rabbit
- Dingo \rightarrow^{-1} Bilby
- Dingo \rightarrow^{-1} Small mammal
- Fox = 1
- Fox \rightarrow^{-1} Bilby
- Cat = 2
- Cat \rightarrow^{-1} Bilby
- Cat \rightarrow^{-1} Small mammal
- Kangaroo = 1
- Kangaroo \rightarrow^{-1} Vegetation
- Rabbit = 2
- Rabbit \rightarrow^{-2} Vegetation
- Rabbit \rightarrow^{+1} Soil
- Bilby = 3
- Bilby \rightarrow^{+2} Soil
- Small mammal = 3
- Small mammal \rightarrow^{-1} Vegetation
- Vegetation = 2
- Vegetation \rightarrow^{+2} Soil
- Soil = 2

- **Dingo = 1**
- Dingo \rightarrow^{-1} Fox
- Dingo \rightarrow^{-1} Kangaroo
- Fox = 3
- Fox \rightarrow^{-1} Rabbit
- Fox \rightarrow^{-1} Small mammal
- Fox \rightarrow^{-1} Cat
- Fox \rightarrow^{-3} Bilby
- Cat = 3
- Cat \rightarrow^{-1} Rabbit
- Cat \rightarrow^{-2} Small mammal
- Cat \rightarrow^{-2} Bilby
- Kangaroo = 3
- Kangaroo \rightarrow^{-3} Vegetation
- Rabbit = 3
- Rabbit \rightarrow^{-3} Vegetation
- Small mammal = 2
- Bilby = 1
- Vegetation = 1
- Vegetation \rightarrow^{+1} Soil
- Soil = 1

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