

1 **TITLE PAGE**

2 **Title**

3 Invasive species-driven trophic cascades: Are cane toads indirectly contributing to small
4 mammal collapses across tropical Australia?

5

6 **Short running title**

7 Ecosystem impacts of cane toads

8

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28

29 **Abstract**

30 Apex predators are fundamentally important in regulating many ecosystems, and
31 perturbations of their populations are frequently implicated in ecosystem declines or
32 collapses. In considering small mammal declines in northern Australia, most attention has
33 focused on interactions between a mammalian apex predator—the dingo *Canis dingo*—and a
34 meso-predator, the feral cat—*Felis catus*. Little consideration has been given to the possible
35 implications of changed reptilian predator assemblages resulting from invasion by a toxic
36 anuran invader, the cane toad (*Rhinella marina*), on small mammals. We used reptile removal
37 records from licenced reptile catchers in three widely spaced towns in the savannas of
38 northern Australia to explore potential impacts of toads on apex and meso-predatory snakes
39 and large lizards. In addition, simultaneous fauna survey data from one town with reptile
40 removal records, coinciding with toad invasion, were used to identify cascading impacts
41 through the savanna ecosystem. Intervention analyses revealed empirical linkages between
42 toad invasion, apex predator declines, meso-predator increases and declines of small
43 mammals and other prey groups. Based on the timing and strength of intervention we
44 postulate a novel conceptual model linking recent mammal declines with trophic cascades
45 following toad invasion, where the loss of large, anurophagous (toad-eating) reptilian apex
46 predators allowed increases in mammal-eating meso-predatory snakes. The conceptual model
47 is discussed in relation to prevailing hypotheses regarding northern Australia's dramatic
48 small mammal declines. Future studies will need to quantify these putative interactions and
49 test their comparative importance so that appropriate management can be implemented to
50 stem the ongoing losses of mammal fauna.

51

52 **Keywords**

- 53 Meso-predator release, apex predators, invasion ecology, ecosystem cascade, tropical
- 54 savanna

56 **INTRODUCTION**

57 *"We were the Leopards, the Lions; those who'll take our place will be little jackals, hyena -*
58 *and sheep", Giuseppe Tomasi di Lampedusa (The Leopard)*

59 The importance of apex predators and their interactions with smaller meso-predators in
60 maintaining global ecosystems has received increasing attention in recent decades. Meso-
61 predator suppression by apex predators is widespread both geographically and taxonomically
62 [1]. Apex predators clearly play a crucial role in maintaining many ecosystems [1], but debate
63 continues about how pervasive their effects are [2-3]. In Australia, for example, several
64 studies suggest that a mammalian apex predator, the dingo *Canis dingo*, suppresses feral cat
65 *Felis catus* activity and the impacts of the latter on native species [4-8], but other work
66 contests this [3]. The influence of apex predators may change depending on the number of
67 different sized meso-predators within predator hierarchies, leading to different outcomes for
68 prey populations [9]. One important lesson from classic predatory studies (e.g. wolves, moose
69 and bears in North America) [10] is that all relevant predators must be considered to achieve
70 a full mechanistic understanding of prey dynamics.

71

72 Meso-predatory interactions have been reported most commonly among mammalian
73 predators, raptors, and in marine systems [1]. In recent years, however, meso-predator release
74 within reptilian predator assemblages has been identified in northern Australian savanna
75 ecosystems resulting from invasion by a toxic anuran, the cane toad *Rhinella marina* [11-15].
76 Here, losses of large reptilian apex predators – varanid species – due to post-ingestion
77 poisoning by toads, have resulted in measurable increases among smaller, meso-predatory
78 reptiles which presumably had been eaten by varanids [11-13]. Despite the rarity of
79 comparable examples [but see 16-17], it is not surprising that this case of reptilian meso-

80 predator release was identified in Australia given the relative abundance of large reptiles in
81 Australian ecosystems, as well as the paucity of large mammalian predators [18]. However, it
82 remains unclear whether meso-predator release among reptiles might have wider implications
83 within the tropical savanna [14, 19].

84

85 Recent rapid and dramatic collapses of small to medium-sized mammals in northern Australia
86 [20-21] continue to puzzle ecologists, although local declines here have been foreshadowed
87 for several decades [22-26]. Recent thinking concerning these declines implicates feral cats
88 interacting with changed fire regimes, large herbivores, and possibly ecosystem condition/
89 productivity, to negatively affect small mammals [4, 25, 20, 27-30, 21, 31]. Cats (along with
90 foxes *Vulpes vulpes* in sub-tropical regions) are thought to have been the primary drivers of
91 historical extinction events across Australia, particularly in arid regions where arrival of cats
92 often coincided with sudden mammal declines even before European settler arrival or the
93 operation of other threatening processes [32, 4]. However, there is little direct evidence to
94 link recent accelerated collapses of northern Australian mammal assemblages in the first
95 decade of the twenty-first century to cat predation. Cats coexisted with susceptible mammals
96 here for a century [33] prior to the recent collapses [34, 20] and there is no evidence that
97 recent changes in cat populations, fire or grazing regimes coincide with these sudden
98 declines. Experimental studies have shown that cat predation can cause local extinctions of
99 rodents inside fenced savanna areas [27, 35], and convergence of cats at recently burnt areas
100 [28, 30] can dramatically increase predation-related mortality of small mammals [31]. There
101 is also a link between more severe fire regimes and lower mammal abundance/richness [34,
102 36-37]. However, these studies do not establish that cat and fire interactions have caused
103 mammal collapses at regional scales [38]. There is no evidence currently available showing

104 that cat populations or predation pressure have increased at the same time that mammal
105 declines were occurring. There are also no data to link any sudden exacerbation of
106 fire/grazing related disturbance regimes at regional levels with recent observed mammal
107 declines. Thus, there is no empirical evidence to directly link recent mammal collapses in the
108 Northern Territory [34, 20-21] with changes in the operation of any known threatening
109 processes (e.g. cats, fire regimes, large herbivores) at the same time that the observed
110 mammal declines occurred.

111

112 One factor acknowledged as potentially influencing mammal assemblages, but for which
113 little evidence has been adduced, is invasion by the cane toad [20-21]. Clear evidence links
114 recent declines of one mammal species, the northern quoll, *Dasyurus hallucatus*, to the
115 arrival of the cane toad [39-40]. Quolls actively hunt and ingest toads and are subject to high
116 rates of mortality due to lethal poisoning [40-41]. However, declines among other small
117 mammals have not been linked to toad arrival. This is because most mammals do not eat cane
118 toads, or escape poisoning by avoiding the toxic glands [40]. Similarly, small mammals are
119 not known to be eaten by cane toads [39].

120

121 In this paper we present a new hypothesis explaining recent north Australian small mammal
122 declines based on observed changes seen in savanna fauna following invasion by cane toads
123 at three separate locations across north-western Australia. The hypothesis is that recent
124 mammal collapses, since 2005 in the Northern Territory, and since 2010 in Western
125 Australia, may be attributable to the arrival of cane toads via a series of cascading impacts on
126 reptilian predator assemblages including mammal-eating species. Changes following cane
127 toad invasion included an immediate decline of large-gaped, large-bodied, generalist

128 (partially anurophagous and reptile-eating) elapid snakes such as the king brown snake
129 (*Pseudechis australis*) and varanid lizards (from here referred to as apex predators) as seen
130 during previous studies [15, 39, 42]. We interpret these collapses as due to poisoning upon
131 ingestion of toxic cane toads [39, 15]. Another change at study sites was an immediate
132 increase among smaller-gaped, smaller-bodied (i.e. meso-predatory), dietary specialist
133 snakes, lizards and anurans, including mammal-eating pythonid and cobubrid snakes.
134 Increases among meso-predatory reptiles was also previously reported in several studies [11-
135 13, 19]. We interpret increases as due to a meso-predator release following loss of large
136 generalist apex reptilian predators [15]. Additional changes associated with cane toad
137 invasion at one of our study sites where we had continuous fauna monitoring data were
138 declines among fauna which is prey to meso-predatory reptiles. Prey included small
139 mammals, very small skinks (< 8 cm long) and many invertebrates. Declines among
140 invertebrates following toad invasion has been reported before [43], though this was
141 interpreted as due to an increase in predator biomass due to cane toad presence, not due to
142 general increases among a range of meso-predators. We interpret declines among prey groups
143 as being driven by increases among their meso-predators, including mammal- and lizard-
144 eating snakes, medium-sized lizards and frogs, as these species all increased following cane
145 toad invasion. We synthesise these empirical observations in the form of a conceptual model
146 that articulates the trophic links between small mammals, cane toads and reptilian predators
147 (Fig. 1). This provides us with a complementary hypothesis to the cat – fire/disturbance
148 driven hypothesis that has dominated the literature on north Australian mammal declines over
149 the last decade [4, 27, 36, 21, 30].

150

151 **METHODS**

152 *Study areas*

153 The main study location was the town of Kununurra (2016 census population 5,300) and its
154 surrounding savanna landscapes including Mirima National Park in far north-eastern Western
155 Australia (Fig. 2a, b). The region has a tropical monsoonal climate, with high temperatures
156 year-round (daily mean maximum 29.6-36.0 °C), and rainfall (913 mm annually) occurring
157 predominantly from November to April. Several tropical savanna habitats occur around
158 Kununurra. Aside from urban and agricultural (broad-acre cropping) habitats, these include
159 black soil plains, eucalypt woodlands dominated by tussock grasses, pindan (*Acacia tumida*)
160 savanna woodlands dominated by *Triodia* hummock grasses and annual *Sorghum* on
161 sandplain, and shrub/*Triodia* spp. dominated woodland on rocky sandstone. Kununurra is
162 adjacent to perennial riparian habitats and permanent water due to the damming of the Ord
163 River (Fig. 2a, b). Minor study locations at Katherine (popn. 6,300) and Darwin (popn.
164 136,800) in the Northern Territory have similar tropical monsoonal climates to Kununurra
165 (Fig. 2a), with daily mean maximum temperatures of 30.1–37.7 °C (Katherine) and 30.6–33.3
166 °C (Darwin), and mean annual rainfalls of 1023 mm and 1729 mm respectively. Both towns,
167 like Kununurra, are small and are predominantly surrounded and interspersed by tropical
168 savanna habitats.

169

170 *Reptile removal records*

171 Removal records of reptiles were obtained from Kununurra, Katherine and Darwin. Trained
172 personnel (government officers or volunteers) in these towns remove snakes and other
173 reptiles when requested by members of the public. Reptile removal records for Kununurra
174 were consistently kept from 2006 prior to cane toad invasion in 2010, through to 2017,
175 encompassing both pre- and post-invasion periods (Fig. 2b). Wildlife officers are compelled

176 to attend snake callouts for reasons of public safety, so data can be considered representative
177 of snake occurrences in the town. Records included date and time of removal, the officer's
178 name who attended, the location/address, the species and size (length) of the animal removed.
179 Data are presented as monthly counts for analysis. In Katherine, snake removal records were
180 available from 1998 to 2008 and covered the pre-invasion (1998-2000) to post-cane toad
181 invasion (2001-2008) periods. Darwin snake removal data were available more sporadically
182 during nine non-consecutive years encompassing pre- and post-invasion by toads. Annual
183 species counts were made for 1997, 1998 and 1999 prior to toad invasion. Records including
184 attending officer, date, time, address, actions and species were kept for the post-toad period in
185 2005, and then annually from 2011 to 2015. Despite the potential for species and habitat bias
186 in the wildlife removed from urban/rural environments in towns [44], we assume that the
187 reptile data represent surrounding savannas because of the small size and isolation of these
188 towns within the vast expanse of uninhabited savannas across the whole of northern Australia
189 (Fig. 2a). This assumption is supported by records of species identities, as most snakes and
190 other reptiles removed were common species characteristic of northern Australian savanna
191 assemblages [45].

192

193 *Fauna surveys*

194 To obtain additional information on predators, and to sample populations of potential prey,
195 we conducted fauna surveys at 15 sites in Mirima NP, Kununurra, from 2006 to 2017 (see
196 Fig. 2a). This period encompassed both pre- and post-cane toad invasion. Mammal trapping
197 data from Elliott and pitfall trap surveys were available for 23 months, though not all sites
198 could be surveyed every month due to logistical constraints (Table S1). Surveys at sites m, n
199 and o in Jul 2006, Jan and Sep 2007, May 2008, Mar and Apr 2017 (Table S1) used 50 × 50

200 m quadrats and 20 Elliott traps (alternating large $15 \times 15.5 \times 46$ cm and medium $9 \times 10 \times 33$
201 cm traps) around the perimeter and 10 pitfall traps (20 cm diameter, 60 cm deep) placed
202 along two parallel drift fence-lines [34, 26]. Mammal surveys at sites a, b, c, d, e, f, g, h, i, j,
203 k and l from Mar 2010 to Apr 2017 (Table S1) used a 40×100 m grid with 18 Elliott traps
204 (alternate 9 large and 9 medium traps) placed 20 m apart in the grid and 4 pitfall traps (29 cm
205 diameter 40 cm deep) placed at each corner with 4 shallow trenches (5 to 15 cm deep)
206 directing animals into traps [46]. Mammal surveys occurred for either 4 or 7 nights. All
207 mammals were identified to species, weighed, head and body length measured, and marked
208 prior to release (permanent marker on ear). Recaptures were not counted. Mammal data are
209 presented as total mammals per 1000 trap nights to standardise them; low numbers for
210 individual mammal species represented in the surveys (Table S2) precluded species analyses.

211

212 Funnel trapping was used to survey reptile, frog and invertebrate assemblages during 25
213 months between Jul 2008 and Apr 2017 (Table S1). A 40×100 m survey grid was used with
214 18 funnel traps ($18 \text{ cm} \times 60 \text{ cm}$) placed 20 m apart within the grid (Radford & Fairman,
215 2015). Funnel traps were placed in the middle of a 6 m long shallow trench (5 to 15 cm deep)
216 to attract and direct animals into traps. All reptiles and frogs were identified to species and
217 snout vent and tail length measured; animals were marked (permanent marker pen) prior to
218 release to establish recaptures. Insects (> 5 mm long) were identified to Order or Family, and
219 other invertebrates to Class or Order. Vertebrate species and invertebrate taxa were
220 categorized according to trophic roles for analysis depending on their diets [47-52, 45].
221 Counts of reptile, frog and invertebrate species/taxa per trap session were recorded and used
222 in analyses. For mammal, reptile, frog and invertebrate taxa we consider all Mirima survey
223 sites, irrespective of survey methodology, to be sampling replicates for the sake of the

224 analyses due to similarities in productivity and geology (sand or sandstone), vegetation
225 (hummock savanna woodland/shrubland) and fauna assemblages.

226

227 *Arrival of cane toads*

228 The arrival month of cane toads in Kununurra was set as the date when animals were first
229 placed in bins at drop-off points by members of the public. The first records of toads in
230 Kununurra were in April 2010. A second arrival date was set at the Mirima NP fauna survey
231 sites adjacent to Kununurra when the first toads appeared in survey traps in April 2011 [46].
232 Cane toads first arrived in Katherine in 2001 and in Darwin in 2005 (T. Parkin, G. Gillespie,
233 unpublished data).

234

235 *Statistical modelling*

236 Species with fewer than 20 records were not included in modelling analyses. We used `tscount`
237 [53] in R version 3.5.1 [54] to fit generalised linear models to our time series count data for
238 each species or species group at different sites, i.e. integer-valued GARCH log-linear models
239 with logarithmic link. In this way, the conditional mean could be linked to potential
240 covariates (e.g. rainfall, temperature, etc., Table S2) and past values or past observations (i.e.
241 previous means). We captured short range serial dependence using a first order
242 autoregressive term on the previous observation (`beta_1`) and yearly seasonality using a 12th
243 order autoregressive term (`alpha_12`). Either a Poisson, or in the case of over-dispersion, a
244 negative binomial conditional distribution, was chosen. Model fit and assessment were based
245 on probability integral transform histograms, the autocorrelation function (ACF) of response
246 residuals, and a cumulative periodogram of Pearson residuals. Using backward stepwise

247 elimination, covariates were excluded on improvement in the model Akaike Information
248 Criterion and only significant covariates (of those listed in Table S2) were included in final
249 models (Table 1). Autoregressive terms were adjusted if the ACF plot indicated subsequent
250 autocorrelation beyond beta_1 and alpha_12.

251

252 To identify shifts in faunal count data post-cane toad invasion, we used intervention analyses
253 (R package *tscount*) [53], where intervention, as defined by Fokianos & Fried [55], was
254 included as a covariate in each model. This covariate included an integer vector giving the
255 time when the intervention effect occurred (τ); in our case, τ differed for each sample site
256 depending on when toads arrived or the detection of a lag in intervention effect. The
257 intervention covariate also included a numeric vector with constants specifying the type of
258 intervention (δ), for $0 < \delta < 1$ the effect decays exponentially and for $\delta = 1$ there is a
259 persistent effect of the intervention after its occurrence). We chose $\delta = 1$ as there was a
260 persistent intervention effect after toad invasion and we were testing for a permanent shift
261 post-intervention. Significance of the intervention effect was assessed for each species using
262 the corresponding confidence intervals of intervention covariate coefficient estimates, and for
263 trophic groups using an intervention test (valid only for long time series or large sample
264 sizes) to test for intervention of type $\delta = 1$ at the time of cane toad invasion.

265

266 **RESULTS**

267 *Reptile removal and fauna survey data*

268 Apex predatory species, including five species of elapid snakes ($n = 364$) and six species of
269 varanids ($n = 42$); meso-predatory species/taxa, including 23 snake ($n = 6584$), nine lizard (n

270 = 561) and seven frog species (n = 487); and prey species/taxa, including five mammals (n =
271 104), six lizards (n = 599) and six invertebrate taxa (n = 1221) were recorded during
272 removals and surveys (Table S2). During Kununurra removals, 328 snakes and reptiles were
273 recorded during 130 consecutive months from Mar 2006 to Dec 2017 (Table S1). In
274 Katherine, 1430 snakes were recorded during 11 years of callouts (1998 to 2008), and in
275 Darwin 5168 snakes and lizards were recorded during nine non-consecutive years (1997-
276 1999, 2005, 2011-2015) (Table S1, S2). In Mirima NP, 2932 reptiles, frogs and invertebrates
277 were recorded during 25 non-consecutive monthly survey periods from 2008 to 2017 (Tables
278 S1, S2). Small mammals were recorded during 23 survey months in Mirima NP between
279 2006 and 2017 (Table S1, S2).

280

281 *Responses to toad invasion among predator and prey groups*

282 As predicted under the conceptual model (Fig. 1), apex predators declined significantly after
283 cane toad invasion, almost all meso-predators increased, and most prey groups – including
284 small mammals – also declined based on intervention tests (Table 1, Figs 3, 4). For combined
285 apex predators in Kununurra, the largest GLM coefficient estimates were for intervention,
286 indicating a strong impact of toad invasion relative to other explanatory variables (Table 1).
287 The strongest additional explanatory variable for apex predators was a 6 month temporal
288 auto-correlative effect indicating a seasonal influence on predator numbers (Table 1, Fig. 3a,
289 Fig. 4a). Intervention (toad invasion) was also significant (marginally) among apex predators
290 in both Darwin and Katherine, with rainfall and monthly autocorrelative terms supported as
291 additional explanatory variables in the model (Table 1).

292

293 Four of the five identified meso-predator groups, including the mammal-eating pythons (Fig.
294 3b), skink-eating elapids, colubrid snakes and combined frogs, agamids and large skinks (Fig.
295 4b), showed significant increasing intervention responses (Table 1). Intervention responses
296 had higher coefficient estimates than for all other explanatory variables for meso-predators,
297 indicating that toad invasion was the strongest predictor of change among these groups
298 (Table 1). All three meso-predatory groups from Katherine and Darwin (mammal-eating
299 pythons, skink-eating elapids and colubrid snakes) also had significant intervention responses
300 (Table 1). The smallest of the identified meso-predators, *Eremiascincus/Heteronotia* (Table
301 S2) had no significant intervention response (Table 1). Additional strongly supported
302 explanatory variables for meso-predatory snakes (pythons, small elapids and colubrids)
303 included seasonal auto-correlation (α_6) and rainfall, and for the frog/agamid/large skink
304 group included rainfall in the previous month, maximum temperature, vegetation cover and
305 time since fire (Table 1).

306

307 Among prey groups, small mammals showed a significant negative response to intervention
308 (invasion) (Table 1, Fig. 3c). Other prey groups (e.g. herbivorous invertebrates (< 3 cm),
309 small skinks, Table S2) also declined significantly post-invasion (Table 1, Fig. 4c).
310 Exceptional among savanna prey groups were larger carnivorous invertebrates (3-12 cm,
311 Table S2) which did not show a significant intervention response (Table 1). In addition to
312 intervention, the strongest explanatory variables for small mammals were rainfall in the
313 previous 2 months, and months since fire (Table 1). Herbivorous invertebrates and small
314 skinks responded most strongly to rainfall in the previous month, seasonal auto-correlation
315 and vegetation cover (Table 1). Large carnivorous invertebrates responded most strongly to

316 seasonal auto-correlation, maximum temperature and rainfall in the previous month (Table
317 1).

318

319 Species-specific apex, meso-predator and prey responses generally conformed to responses
320 predicted in the conceptual model (Fig. 1) with a few minor exceptions (Table S4). Among

321 meso-predatory species, the skink *Eremiascincus isolepis* and gecko *Heterontia binoei*, in

322 Kununurra, showed no intervention responses. These were among the smallest of the meso-

323 predators (13 cm and 9 cm, Table S2) The lesser black whip snake, *Demansia vestigiata*, in

324 Katherine, uniquely among small skink-eating elapids, showed a significant negative

325 intervention response (Table S4). Among small skinks, *Carlia* spp. showed a positive

326 intervention response which was the opposite to small skink responses overall (Table S4).

327 *Carlia* spp. were the largest among the small skinks (ca. 11 cm) with others in the group < 10

328 cm long (Table S2).

329

330 **DISCUSSION**

331 Small mammal declines in northern Australia have not previously been temporally or

332 spatially linked with the arrival of cane toads [34, 20-21], nor to cascading impacts among

333 reptilian predators [14, 19]. To some extent this may have arisen due to small numbers of the

334 larger reptilian predators usually trapped during standard fauna surveys leading to difficulties

335 in detecting trends coinciding with changes among smaller more numerous species including

336 mammals. In this study we present simultaneous data on large reptilian predator assemblages

337 using novel wildlife removal data alongside standard fauna monitoring data collected at the

338 same time and place. These combined data reveal multiple and pervasive ecosystem-wide

339 trends coincident with cane toad invasion which have not previously been apparent from

340 standard surveys alone. The trends identified in this study are consistent with the hypothesis
341 that cane toad invasion initiates ecosystem-wide trophic cascades (Fig. 1), as suggested by
342 Doody et al. [14] and Feit et al. [19]. These trophic cascades include the functional loss of
343 keystone apex reptilian predators including large-gaped elapid snakes [42] and large varanid
344 lizards (*Varanus* spp); a meso-predatory release of smaller-gaped predominantly mammal-
345 and skink-eating snakes (pythons, colubrids and small elapids) [15] and invertebrate-eating
346 predators (e.g. frogs and agamid and large scincid lizards); and finally a decline among
347 savanna prey groups including small mammals, smaller skinks and invertebrates, resulting
348 from increased predation pressure by meso-predators (Fig. 1). Although previous studies
349 have speculated that there may be a link between toad-driven changes to predator
350 assemblages and small mammal declines [21], this is the first study to empirically link
351 temporal and spatial data on toad invasion, reptilian predator assemblage change and small
352 mammal declines.

353

354 Although the conceptual model presented here (Fig. 1) seems plausible, is partially supported
355 by literature [39, 15, 14] and we have temporal and spatial links between mammal declines
356 and toad invasion from Kununurra (Table 1), it is unclear if observed historical patterns of
357 mammal decline align with sequential timing of toad invasions across northern Australia?
358 Unfortunately monitoring programs for large reptilian predators and savanna fauna generally
359 were not widespread, co-ordinated or sometimes even initiated prior to 2001-2005 [56] when
360 cane toads first appeared in the Katherine/Darwin region (Fig. 2a). Therefore, there is little
361 quantitative evidence to link mammal declines, their timing and/or their associated
362 threatening processes [56]. However, it is clear that some northern mammal declines pre-date
363 cane toad arrival. Mammal declines reported at mainland Northern Territory sites up to 2005

364 [23-24, 56-58], pre-2010 in the Kimberley region of Western Australia [22, 25-26], or up to
365 the present on Melville Island [59] cannot be attributed to cane toad invasion because the
366 invader had not yet arrived at these locations (Fig. 2a). However, many of these pre-toad
367 declines affected only some mammal species or groups [22, 26, 56-57, 60-61], were subtle
368 and relatively difficult to detect [23-24] or were based on few temporal data points [59],
369 making it difficult to interpret changes as decline rather than as natural population variability.

370

371 In contrast to the above changes, more recent mammal declines post cane toad invasion in
372 Kakadu and elsewhere in the Northern Territory since 2005 [34, 20, 56, 36, 21, 58] have been
373 pervasive across the entire suite of critical weight range mammal species (mean adult body
374 weight 35 - 5500 g) [62], have involved dramatic population collapses to levels almost
375 beyond detectability, and have been relatively well documented. In addition, mammal
376 abundance ahead of the cane toad invasion in the Kimberley has remained relatively high and
377 stable throughout the same period (e.g. mean trap success 7.24%, as per Radford et al. 2014),
378 until the declines noted in this study in the eastern edge of the Kimberley after cane toads
379 arrived in 2010. In contrast, mammal abundance behind the cane toad front in the Northern
380 Territory has remained consistently very low ever since invasion in 2005 (mean trap success
381 < 1% trap success) [34, 58]. These data collectively support the notion that factors other than
382 cane toads (e.g. cats and disturbance regimes) [4, 21] have been involved in driving small
383 mammal declines across north western Australia pre cane toad invasion, but also that cane
384 toad arrival has led to a recent increase in the pervasiveness of mammal assemblage-wide
385 collapses on top of the previous declines.

386

387 Current thinking pertaining to small mammal declines in northern Australia centres on feral
388 cat predation as a key driver [4, 20-21, 27-28, 31]. However, the cat and cane toad
389 hypotheses are not incompatible and may act as complementary (and cumulative) drivers of
390 mammal declines. The role of cats in northern Australia is seen as an extension of historical
391 nationwide cat- and fox-driven mammal declines and extinctions, especially in the arid zone
392 [4, 32]. However, the cat hypothesis relies on interactions with other factors to be a tenable
393 explanation for northern mammal declines [20-21, 36]. This is because cats apparently
394 coexisted with savanna mammals for over a century before recent north Australian declines
395 [33]. Cat predation is known to interact with high intensity fire regimes to concentrate cat
396 hunting activity [28, 30], and this increases mortality in local mammal populations [29, 31].
397 However, cat predation pressure is also thought to be influenced by apex predators, in
398 particular the dingo (*Canis dingo*) [4-6]. High density of dingoes in high rainfall, high
399 productivity areas of the Kimberley has been argued to reduce predation impacts by meso-
400 predatory cats [5, 26]. However, cats are also known anecdotally to be depredated by large
401 reptilian predators (and also to eat reptiles) [63]. As meso-predators, cats too may benefit
402 from cane toad driven declines of apex reptilian predators, similar to those recorded here
403 among meso-predatory snakes, lizards and frogs (Table 1). Future research is required to
404 examine interactions between cane toad invasion, reptilian predator cascades and their
405 interactions with cat impacts on small mammals if a greater understanding of mammal
406 declines in northern Australia is to be achieved.

407

408 The conceptual model presented in this study has empirical support, highlighting the timing
409 and apparent strength of observed trends associated with cane toad invasion. However,
410 raising conceptual models/hypotheses to explain observed patterns is only one step in the

411 process of establishing a model's efficacy. The next step is for the conceptual model to be
412 subject to tests, or falsified, to enable us to evaluate further if the hypothesis provides a
413 tenable explanation for mammal declines relative to other hypotheses. Future research is
414 needed on meso-predatory snake densities and predation rates to test whether predation by
415 these reptilian predators is sufficient compared to that of cats to cumulatively drive mammal
416 declines. Recently, estimates of cat densities and predation rates were made across the
417 continent [63-66], including the Kimberley region [29]. Equivalent estimates are not
418 available for reptilian predators and their impacts on mammals. What fragmentary data we
419 have on snake densities and home ranges [67-70] suggest much greater densities of snakes
420 than for cats and also much smaller home ranges. This means that even if snake ingestion
421 rates are much lower than for cats, they may cause comparable overall predation pressure.
422 We know that snakes in some cases can have very large impacts on mammalian and avian
423 assemblages. These include one meso-predatory snake from this study (e.g. *B. irregularis*)
424 [16]. In addition, there is information from a cat exclosure experiment in northern Australia
425 [35] that showed similar predation by pythons on savanna rodents to that by cats. However,
426 the hypothesis that reptilian predation could be equivalent to that of feral cats, and the
427 possibility that cumulative impacts could be substantial, needs to be tested more widely
428 across Australian savanna landscapes if we are to establish its plausibility in playing part in
429 regional mammal declines.

430

431 Another test to validate the role of cane toad cascades in driving mammal declines, is whether
432 ongoing toad invasion across the Kimberley leads to rolling changes among reptilian (and
433 mammalian) predator assemblages and to continuing mammal losses. Following initial cane
434 toad arrivals in Kununurra/East Kimberley in 2009/2010, cane toads have now spread to

435 Purnululu National Park in the south east Kimberley (ca. 2012), to Drysdale River National
436 Park in the north Kimberley (ca. 2016), and to the far north Kimberley at Mitchell River
437 National Park (ca. 2019) (Fig. 2a). If cane toad initiated cascades are a key factor driving
438 mammal declines, we should expect mammal monitoring programs at these locations to
439 reveal further declines within five years to one decade following toad arrival. Already the
440 limited data from Purnululu National Park (Fig. 2a) indicates a ca. 90% decline in mammal
441 trap success following toad invasion, with pre-toad trap success recorded at 1.4 % in 1989
442 [71], 1.5 % in 2004/2005 [72] and 3.7% in 2008 [26] prior to toads; at 2.5 % one year
443 following cane toad arrival in 2013 (Fig. 2a); and then down to 0.42 % and 0.25 % in 2016
444 and 2017 four and five years post-invasion (I.J. Radford and B. Corey, unpublished data).
445 Documentation of sequential reptilian predator changes associated with mammal declines and
446 toad invasion in the wake of cane toad invasion fronts moving across the Kimberley would
447 provide further empirical evidence for the role of cane toads in driving recent mammal
448 declines. Ideally, these empirical studies of temporal and spatial changes coincident with cane
449 toad invasion would be accompanied by experimental exclosure studies, similar to those
450 conducted for cat impacts on mammals [27, 73, 58, 35], to test the plausibility and magnitude
451 of reptilian predator impacts on mammals in both pre- and post-invasion savanna ecosystems.

452

453 This study joins others in highlighting the potential importance of reptilian predators, and
454 reptilian meso-predator release, in the functioning of Australian and global ecosystems [1, 14,
455 16-17, 74]. One of the meso-predatory species implicated here in driving mammal declines,
456 *Boiga irregularis*, is already documented as having driven catastrophic declines and
457 extinctions of an entire avian forest assemblage, as well as small mammals, on the island of
458 Guam [16]. It is perhaps not surprising that, in a continent with very high reptilian diversity

459 [74-75] and several reptilian niche equivalents of mammalian predators elsewhere [18], as
460 well as extensive pre-historical extinctions of most large mammal species [4], that reptile
461 predators play such an ostensibly prominent role in Australian ecosystems.

462

463 REFERENCES

- 464 1. Ritchie EG, Johnson CN. Predator interactions, mesopredator release and biodiversity
465 conservation. *Ecology Letters*. 2009;12:982-998.
- 466 2. Garrott RA, Gude JA, Bergman EJ, Gower C, White PJ, Hamlin KL. Generalizing wolf
467 effects across the Greater Yellowstone Area: a cautionary note. *Wildlife Society*
468 *Bulletin*. 2005;33:1245-1255.
- 469 3. Allen BL, Engeman RM, Allen LR. Wild dogma: an examination of recent “evidence”
470 for dingo regulation of invasive mesopredator release in Australia. *Current Zoology*.
471 2011;57:568-583.
- 472 4. Johnson C. Australia's mammal extinctions: a 50,000-year history. Cambridge University
473 Press. 2006.
- 474 5. Kennedy M, Phillips BL, Legge S, Murphy SA, Faulkner RA. Do dingoes suppress the
475 activity of feral cats in northern Australia? *Austral Ecology*. 2012;37:134-139.
- 476 6. Letnic M, Ritchie EG, Dickman CR. Top predators as biodiversity regulators: the dingo
477 *Canis lupus dingo* as a case study. *Biological Reviews*, 2012;87:390-413.
- 478 7. Newsome TM, Ballard G-A, Crowther MS, Dellinger JA, Fleming PJS, Glen AS, et al.
479 Resolving the value of the dingo in ecological restoration. *Restoration Ecology*.
480 2015;23:201-208.
- 481 8. Leo V, Reading RP, Gordon C, Letnic M. Apex predator suppression is linked to
482 restructuring of ecosystems via multiple ecological pathways. *Oikos*. 2018;

- 483 9. Levi T, Wilmers CC. Wolves–coyotes–foxes: a cascade among carnivores. *Ecology*.
484 2012;93:921-929.
- 485 10. Krebs CJ. *The Ecological World View*. University of California Press. 2008
- 486 11. Doody JS, Green B, Sims R, Rhind D, West P, Steer D. Indirect impacts of invasive cane
487 toads (*Bufo marinus*) on nest predation in pig-nosed turtles (*Carettochelys insculpta*).
488 *Wildlife Research*. 2006;33:349-354.
- 489 12. Doody JS, Green B, Rhind D, Castellano CM, Sims R, Robinson T. Population-level
490 declines in Australian predators caused by an invasive species. *Animal Conservation*.
491 2009;2:46-53.
- 492 13. Doody JS, Castellano CM, Rhind D, Green B. Indirect facilitation of a native
493 mesopredator by an invasive species: are cane toads re-shaping tropical riparian
494 communities? *Biological Invasions*. 2013;15:559-568.
- 495 14. Doody SJ, Rhind D, Green B, Castellano C, McHenry C, Clulow S. Chronic effects of an
496 invasive species on an animal community. *Ecology*. 2017;10:1002/1889.
- 497 15. Feit B, Letnic M. Species level traits determine positive and negative population impacts
498 of invasive cane toads on native squamates. *Biodiversity and Conservation*.
499 2015;24:1017-1029.
- 500 16. Savidge JA. *The Role of Disease and Predation in The Decline of Guam's Avifauna*
501 *(Extinction, Boiga Irregularis)* Doctoral dissertation, University of Illinois at Urbana-
502 Champaign. 1986.
- 503 17. Dorcas ME, Willson JD, Reed RN, Snow RW, Rochford MR, Miller MA, et al. Severe
504 mammal declines coincide with proliferation of invasive Burmese pythons in Everglades
505 National Park. *Proceedings of the National Academy of Sciences*. 2012;109:2418-2422.
- 506 18. Sweet SS, Pianka ER. Monitors, mammals and Wallace's Line. *Mertensiella*.
507 2007;16:79-99.

- 508 19. Feit B, Gordon CE, Webb JK, Jessop TS, Laffan SW, Dempster T, Letnic M. Invasive
509 cane toads might initiate cascades of direct and indirect effects in a terrestrial ecosystem.
510 *Biological Invasions*. 2018;10.1007/s10550-018-1665-8.
- 511 20. Woinarski JCZ, Legge S, Fitzsimons JA, Traill BJ, Burbidge AA, Fisher A, et al. The
512 disappearing mammal fauna of northern Australia: context, cause, and response.
513 *Conservation Letters*. 2011;4:192-201.
- 514 21. Ziembicki MR, Woinarski JCZ, Webb JK, Vanderduys E, Tuft K, Smith J, et al.
515 Stemming the tide: progress towards resolving the causes of decline and implementing
516 management responses for the disappearing mammal fauna of northern Australia.
517 *THERYA*. 2015;6:169-225.
- 518 22. McKenzie NL. Mammals of the Phanerozoic south-west Kimberley, Western Australia:
519 biogeography and recent changes. *Journal of Biogeography*. 1981;8:263-280.
- 520 23. Braithwaite RW, Muller WJ. Rainfall, groundwater and refuges: predicting extinctions of
521 Australian tropical mammal species. *Austral Ecology*. 1997;22:57-67.
- 522 24. Woinarski JCZ, Milne DJ, Wanganeen G. Changes in mammal populations in relatively
523 intact landscapes of Kakadu National Park, Northern Territory, Australia. *Austral*
524 *Ecology*. 2001;26:360-370.
- 525 25. McKenzie NL, Burbidge AA, Baynes A, Brereton RN, Dickman CR, Gordon G, et al.
526 Analysis of factors implicated in the recent decline of Australia's mammal fauna. *Journal*
527 *of Biogeography*, 2007; 34:597-611.
- 528 26. Radford IJ, Dickman CR, Start AN, Palmer C, Carnes K, Everitt C, et al. Mammals of
529 Australia's tropical savannas: a conceptual model of assemblage structure and regulatory
530 factors in the Kimberley region. *PLOS ONE*. 2014;9:0092341.

- 531 27. Frank A, Johnson CN, Potts JM, Fisher A, Lawes MJ, Woinarski JCZ, et al.
532 Experimental evidence that feral cats cause local extirpation of small mammals in
533 Australia's tropical savannas. *Journal of Applied Ecology*, 2014;51:1486-1493.
- 534 28. McGregor HW, Legge S, Jones ME, Johnson CN. Landscape management of fire and
535 grazing regimes alters the fine-scale habitat utilisation by feral cats. *PLOS ONE*.
536 2014;9:e109097.
- 537 29. McGregor HW, Legge S, Potts J, Jones ME, Johnson CN. Density and home range of
538 feral cats in north-western Australia. *Wildlife Research*. 2015;42:223-231.
- 539 30. McGregor HW, Legge S, Jones ME, Johnson CN. Extraterritorial hunting expeditions to
540 intense fire scars by feral cats. *Scientific Reports*. 2016;6:22559.
- 541 31. Leahy L, Legge SM, Tuft K, McGregor HW, Barmuta LA, Jones ME, Johnson, C. N.
542 Amplified predation after fire suppresses rodent populations in Australia's tropical
543 savannas. *Wildlife Research*. 2016;42:705-716.
- 544 32. Dickman CR. Overview of the impacts of feral cats on Australian native fauna.
545 Canberra: Australian Nature Conservation Agency. 1996;1-92.
- 546 33. Abbott I. Origin and spread of the cat, *Felis catus*, on mainland Australia, with a
547 discussion of the magnitude of its early impact on native fauna. *Wildlife Research*.
548 2002;29:51-74.
- 549 34. Woinarski JCZ, Armstrong M, Brennan K, Fisher A, Griffiths AD, Hill B, et al.
550 Monitoring indicates rapid and severe decline of native small mammals in Kakadu
551 National Park, northern Australia. *Wildlife Research*. 2010;37:116-126.
- 552 35. Tuft K, Legge S, Frank ASK, James AI, May, T, Page E, Radford IJ, et al. Further
553 experimental evidence that feral cats cause local extirpation of small mammals in
554 Australia's tropical savannas. *Journal of Applied Ecology*

- 555 36. Lawes MJ, Murphy BP, Fisher A, Woinarski JC, Edwards AC, Russell-Smith J. Small
556 mammals decline with increasing fire extent in northern Australia: evidence from long-
557 term monitoring in Kakadu National Park. *International Journal of Wildland Fire*.
558 2015;24:712-722.
- 559 37. Radford IJ, Gibson LA, Corey B, Carnes K, Fairman R. Influence of fire mosaics, habitat
560 characteristics and cattle disturbance on mammals in fire-prone savanna landscapes of
561 the northern Kimberley. *PLOS ONE*, 2015;10(6):p.e0130721.
- 562 38. Andersen AN, Cook GD, Corbett LK, Douglas MM, Eager RW, Russell-Smith J, et al.
563 Fire frequency and biodiversity conservation in Australian tropical savannas:
564 implications from the Kapalga fire experiment. *Austral Ecology*. 2005;30:155-167.
- 565 39. Shine R. The ecological impact of invasive cane toads (*Bufo marinus*) in Australia. *The*
566 *Quarterly Review of Biology*. 2010;85:253-291.
- 567 40. Pearson DJ, Webb JK, Greenlees MJ, Phillips BL, Bedford GS, Brown GP, Thomas J,
568 Shine R. Behavioural responses of reptile predators to invasive cane toads in tropical
569 Australia. *Austral Ecology*, 2014;39:448-454.
- 570 41. Jolly CJ, Kelly E, Gillespie GR, Philips B, Webb JK. Out of the frying pan:
571 Reintroduction of toad-smart northern quolls to southern Kakadu National Park. *Austral*
572 *Ecology*. 2018;10.1111/aec.12551.
- 573 42. Brown GP, Phillips BL, Shine R. The ecological impact of invasive cane toads on
574 tropical snakes: field data do not support laboratory-based predictions. *Ecology*.
575 2011;92:422-431.
- 576 43. Greenlees MJ, Brown GP, Webb JK, Phillips BL, Shine R. Effects of an invasive anuran
577 [the cane toad (*Bufo marinus*)] on the invertebrate fauna of a tropical Australian
578 floodplain. *Animal Conservation*. 2006;9:431-438.

- 579 44. Shine R, Koenig J. Snakes in the garden: an analysis of reptiles “rescued” by
580 community-based wildlife carers. *Biological Conservation*. 200;102:271-283.
- 581 45. Cogger H. *Reptiles and Amphibians of Australia*. CSIRO Publishing. 2014.
- 582 46. Radford IJ, Fairman R. Fauna and vegetation responses to fire and invasion by toxic cane
583 toads (*Rhinella marina*) in an obligate seeder dominated tropical savanna in the
584 Kimberley, Northern Australia. *Wildlife Research* 2015;42:302–314.
- 585 47. Shine R. Ecology of eastern Australian whipsnakes of the genus *Demansia*. *Journal of*
586 *Herpetology*. 1980;14:381-389.
- 587 48. Shine R, Slip D.J. Biological aspects of the adaptive radiation of Australasian pythons
588 (Serpentes: Boidae). *Herpetologica*. 1990;46:283-290.
- 589 49. Shine R. Strangers in a strange land: ecology of the Australian colubrid snakes. *Copeia*.
590 1991;120-131.
- 591 50. Shine R. Allometric patterns in the ecology of Australian snakes. *Copeia*. 1994;851-867.
- 592 51. Shine R, Madsen T. Prey abundance and reproduction: rats and pythons on a tropical
593 Australian floodplain. *Ecology*. 1997;78:1078-1086.
- 594 52. Zborowski P, Storey R. *A Field Guide to Insects in Australia*. Second Edition. Reed New
595 Holland. 2003.
- 596 53. Liboschik T, Fried R, Fokianos K, Probst P. tscount: Analysis of Count Time Series. R
597 package version 1.3.0. <https://CRAN.R-project.org/package=tscount>. 2016.
- 598 54. R Core Team. R: A language and environment for statistical computing. R Foundation
599 for Statistical Computing, Vienna. <https://www.R-project.org/>. 2018.
- 600 55. Fokianos K, Fried R. Interventions in INGARCH processes. *Journal of Time Series*
601 *Analysis*. 2010;31:210–225.

- 602 56. Ziembicki MR, Woinarski JC, Mackey B. Evaluating the status of species using
603 Indigenous knowledge: Novel evidence for major native mammal declines in northern
604 Australia. *Biological Conservation*. 2013;157:78-92.
- 605 57. Ibbett M, Woinarski JCZ, Oakwood M. Declines in the mammal assemblage of a rugged
606 sandstone environment in Kakadu National Park, Northern Territory, Australia.
607 *Australian Mammalogy*. 2017;doi:10.1071/AM17011.
- 608 58. Stokeld D, Fisher A, Gentles T, Hill B, Triggs B, Woinarski JCZ, Gillespie GR. What do
609 predator diets tell us about mammal declines in Kakadu National Park? *Wildlife*
610 *Research*. 2018;10.1071/WR17101.
- 611 59. Davies HF, McCarthy MA, Firth RSC, Woinarski JCZ, Gillespie GR, Andersen AN, et
612 al. Declining populations in one of the last refuges for threatened mammal species in
613 northern Australia. *Austral Ecology*. 2018;doi:10.1111/aec.12596.
- 614 60. Palmer C, Taylor R, Burbidge AA. Recovery Plan for the Golden Bandicoot, *Isodon*
615 *auratus*, and Golden-backed Tree-rat, *Mesembriomys macrurus*, 2004-2009. Department
616 of Infrastructure, Planning & Environment; 2003.
- 617 61. Woinarski JC, Burbidge AA, Harrison PL. The action plan for Australian mammals
618 2012.
- 619 62. Burbidge AA, McKenzie NL. Patterns in the modern decline of Western Australia's
620 vertebrate fauna: causes and conservation implications. *Biological conservation*.
621 1989;50(1-4):143-98.
- 622 63. Woinarski JCZ, Murphy BP, Palmer R, Legge SM, Dickman CR, Doherty TS, et al. How
623 many reptiles and killed by cats in Australia? *Wildlife Research*. 2018;45:247-266.
- 624 64. Legge S, Murphy BP, McGregor H, Woinarski JCZ, Augusteyn J, Ballard G, et al.
625 Enumerating a continental-scale threat: How many feral cats are in Australia? *Biological*
626 *Conservation*. 2017;206:293-303.

- 627 65. Woinarski JCZ, Murphy BP, Legge SM, Garnett ST, Lawes MJ, Comer S, et al. How
628 many birds are killed by cats in Australia? *Biological Conservation*. 2017;214:76-87.
- 629 66. Woinarski JCZ, Legge SM, Dickman CR. *Cats in Australia: companion and killer*.
630 CSIRO Publishing, Melbourne. 2019.
- 631 67. Slip DJ, Shine R. Habitat use, movements and activity patterns of free-ranging Diamond
632 Pythons, *Morelia-spilota-spilota* (Serpentes, Boidae)-a radiotelemetric study. *Wildlife*
633 *Research*. 1988;15(5):515-31.
- 634 68. Madsen T, Shine R. Seasonal migration of predators and Prey - A study of pythons and
635 rats in tropical Australia. *Ecology*. 1996;77(1):149-56.
- 636 69. Brown GP, Shine R, Madsen T. Spatial ecology of slatey-grey snakes (*Stegonotus*
637 *cucullatus*, Colubridae) on a tropical Australian floodplain. *Journal of Tropical Ecology*.
638 2005;21(6):605-12.
- 639 70. Corey B, Doody JS. Anthropogenic influences on the spatial ecology of a semi-arid
640 python. *Journal of Zoology*. 2010;281:293-302.
- 641 71. Woinarski JCZ. The wildlife and vegetation of Purnululu (Bungle Bungle) National Park
642 and adjacent area. *Wildlife Research Bulletin*. 1992(6).
- 643 72. Partridge TB. Fire and Fauna in Purnululu (Bungle Bungle) National Park, Kimberley,
644 Western Australia. PhD Thesis. 2009.
- 645 73. Stokeld D, Gentles T, Young S, Hill B, Fisher A, Woinarski J, Gillespie G. Experimental
646 evaluation of the role of feral cat predation in the decline of small mammals in Kakadu
647 National Park. Final Report. Department of Environment and Natural Resources,
648 Darwin. 2016.
- 649 74. Pianka ER. Diversity and adaptive radiations of Australian desert lizards. In *Ecological*
650 *Biogeography of Australia*. Dr W. Junk Publishers, The Hague. 1981.

- 651 75. Morton SR, James CD. The diversity and abundance of lizards in arid Australia: a new
652 hypothesis. *The American Naturalist*. 1988;132:237-256.
- 653 76. Gelman A. Scaling regression inputs by dividing by two standard deviations. *Statistics in*
654 *Medicine*. 2008;27:2865-2873.

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656 **Data Accessibility Statement**

657 Data from Western Australia and owned by the Department of Biodiversity, Conservation
658 and Attractions can be made available upon request to the first author. Data owned by
659 separate custodians including the Northern Territory's Flora and Fauna Division, Department
660 of Land Resource Management, or Rick Shine from the University of Sydney, would have to
661 be requested separately direct to custodians.

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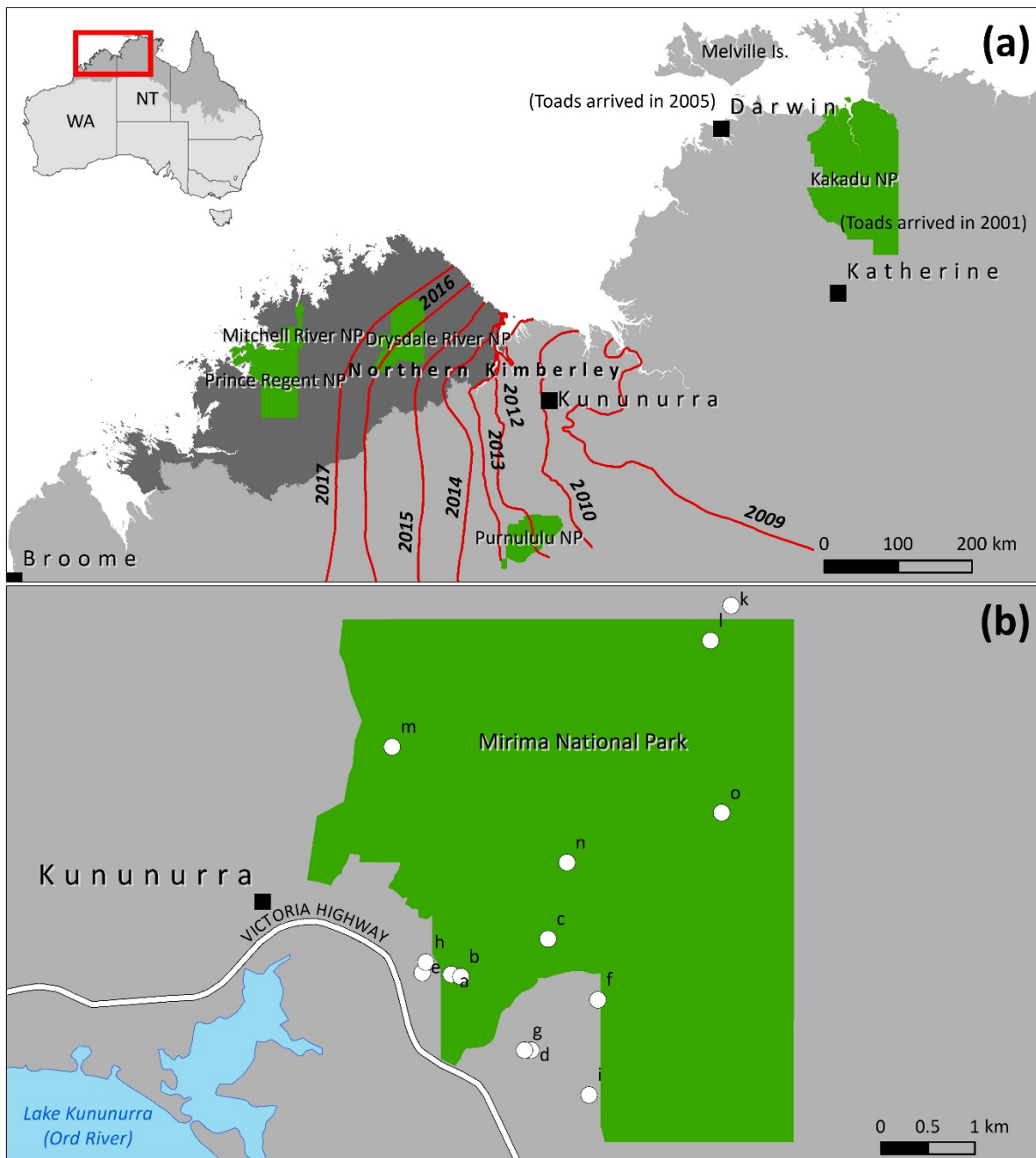
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681 **Figure legends and embedded figures**

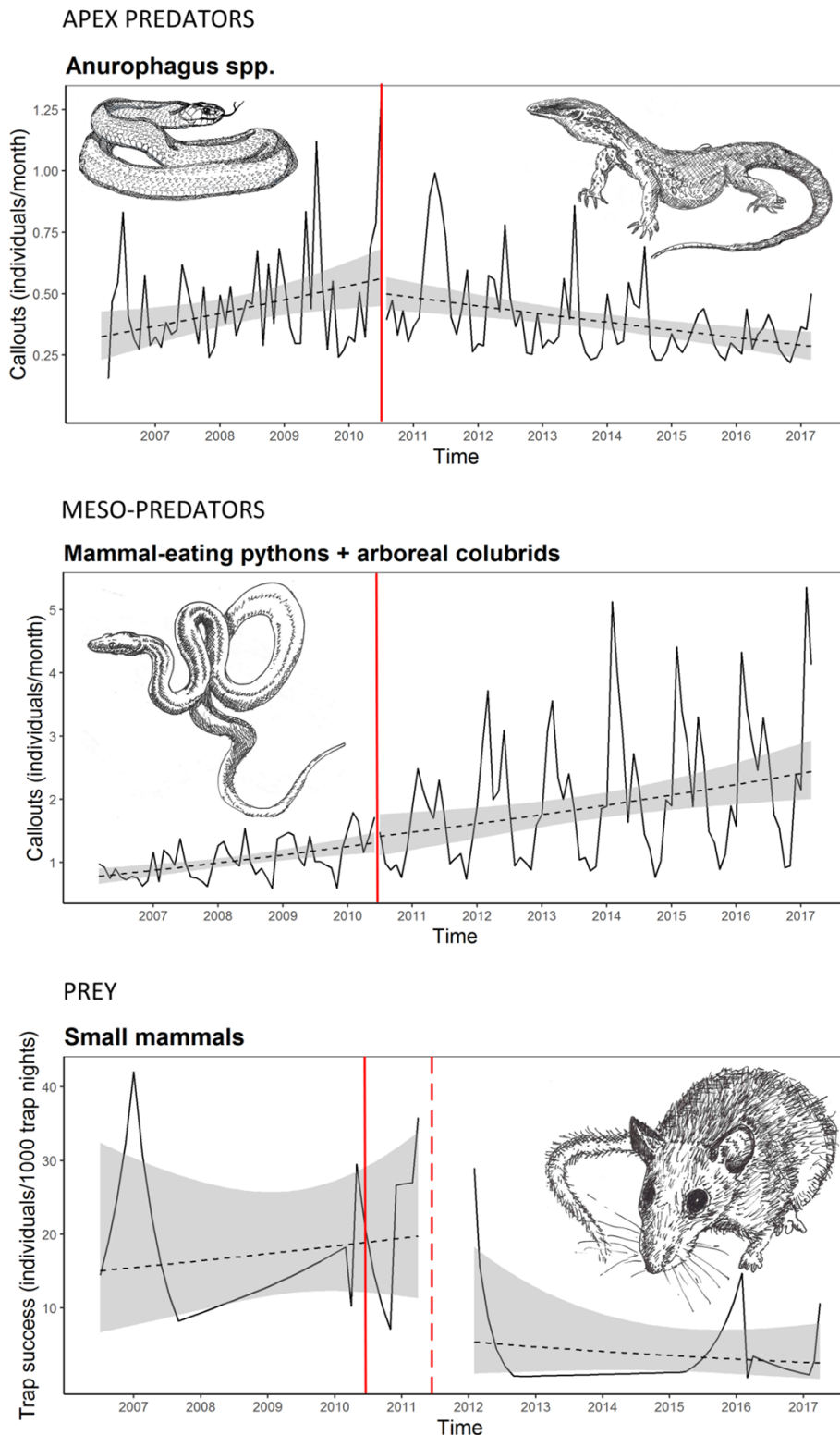


682

683 **Fig. 2** a) North Western Australia including the minor study areas of Katherine and Darwin
684 and b) the main study area of Kununurra and Mirima National Park survey sites (white dots)
685 in the Kimberley region of Western Australia (WA). The red inset (a) shows the study region
686 within the broader savanna biome (darker grey) in Australia. The map also shows sequential
687 invasion of cane toads (*Rhinella marina*) across northern Australia. Cane toads began

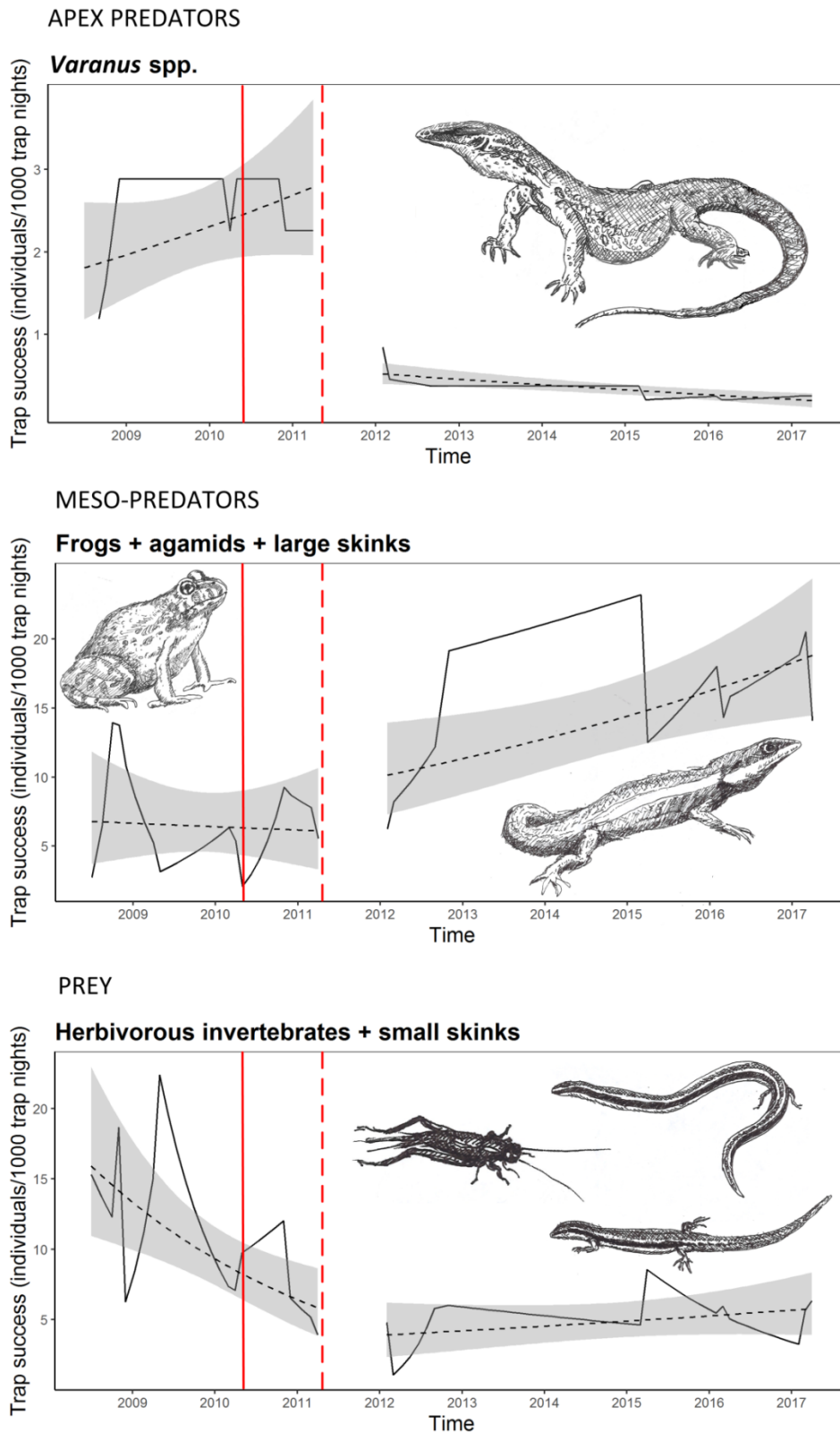
688 arriving in Katherine and Kakadu National Park in the Northern Territory (NT) in 2001 and
689 were in Darwin by 2005. Red contour lines mark the estimated cane toad invasion front
690 annually from the end of 2009, when toads first entered WA from the NT, in 2012 when
691 toads arrived in Purnululu National Park, through to 2016 and 2017 when toads first arrived
692 in the Drysdale River National Park in the North Kimberley bioregion (dark grey). The Cane
693 Toad Strategy for WA 2009-2019 provided annual spatial data on invasion fronts. National
694 Parks are shown in green.

695



696

697 **Fig. 3.** Modelled trends in occurrence before and after cane toad (*Rhinella marina*) invasion for a) apex
698 predators (large anurophagous reptiles and elapids) from Kununurra snake callout records, b) meso-predators
699 (mammal-eating pythons and arboreal colubrids) from Kununurra snake callout records, and c) the small
700 mammal prey group from Mirima fauna surveys. The vertical solid red line indicates the arrival date of toads in
701 Kununurra in 2010 and the dashed red line indicates when toads arrived at fauna survey sites in 2011.



702

703 **Fig. 4.** Modelled trends in occurrence (trap success) before and after cane toad (*Rhinella marina*)
704 invasion for apex predators (large varanid reptiles, *Varanus* spp.), meso-predators (frogs, agamids
705 and large skinks), and prey groups (herbivorous invertebrates and small skinks) from Mirima fauna
706 surveys. The vertical solid red line indicates the arrival date of toads in Kununurra in 2010 and the
707 dashed red line indicates when toads arrived at fauna survey sites in 2011.

708 **Supporting Information**

709 **Table S1.** Mirima NP small mammal (Elliott traps, pit fall traps) and reptile, frog and invertebrate
 710 (funnel traps) fauna survey site numbers, trap effort and site names during months when surveys
 711 were conducted between 2006 and 2017. ¹Denotes the first month when cane toads (*Rhinella*
 712 *marina*) were recorded in drop off points in Kununurra (Intervention 1). ²Denotes when toads first
 713 appeared in survey records at Mirima sites (Intervention 2).

Year	Month	Mammals		Reptiles, Frogs, Invertebrates		Site names
		No. sites	Trap effort	No. sites	Trap effort	
2006	Jul	3	336	-	-	m,n,o
2007	Jan	2	224	-	-	m,n
2007	Sep	1	112	-	-	o
2008	May	1	112	-	-	o
2008	Jul	-	-	3	378	a,b,c
2008	Oct	-	-	2	252	a,b
2008	Nov	-	-	6	756	c,d,e,f,g,h
2008	Dec	-	-	2	252	i,j
2009	Apr	-	-	7	882	a,b,d,e,f,g,j
2009	May	-	-	3	378	c,h,i
2010	Mar	7	432	7	504	a,b,d,e,f,g,h
2010 ¹	Apr	2	288	2	144	c,i
2010	May	1	144	1	72	j
2010	Nov	8	704	8	576	a,c,d,f,g,h,i,j
2010	Dec	2	176	2	144	b,e
2011	Mar	7	616	7	504	a,b,c,d,g,i,j
2011 ²	Apr	3	264	3	216	e,f,h
2012	Feb	6	528	6	432	c,d,f,g,i,j
2012	Mar	4	352	4	288	a,b,e,h
2012	Sep	6	528	6	432	a,b,d,e,g,h
2012	Nov	4	352	4	288	c,f,i,j
2015	Mar	6	528	6	432	c,d,f,g,i,j
2015	Apr	4	352	4	288	a,b,e,h
2016	Feb	6	528	6	432	a,b,e,h,i,j
2016	Mar	2	176	2	144	d,g
2016	Apr	4	352	4	288	c,f,k,l
2017	Feb	2	176	2	144	c,d
2017	Mar	8	644	8	616	a,b,e,g,h,i,j,m
2017	Apr	2	176	2	112	n,f

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Table 1. Level of significance (p-values) of intervention tests conducted at time of cane toad (*Rhinella marina*) invasion (Kununurra 2010, Darwin 2005, Katherine 2001) after fitting time series generalised linear models (INGARCH log-linear models with logarithmic link) on occurrence records of functional groups of apex predators, meso-predators and prey trophic levels at different sites.

Trophic group	Functional group	Study site																		
		Kununurra						Darwin						Katherine						
		Intervention test (p-value)	Coefficients	Estimate	SE	CI (lower)	CI (upper)	Intervention test (p-value)	Coefficients	Estimate	SE	CI (lower)	CI (upper)	Intervention test (p-value)	Coefficients	Estimate	SE	CI (lower)	CI (upper)	
<i>Apex predators</i>																				
	Anurophagous & snake eating elapids + varanids	0.040*						0.097 .						0.085 .						
			(Intercept)	-0.924	0.334	-1.579	-0.270		(Intercept)	5.323	0.914	3.531	7.115		(Intercept)	1.971	0.720	0.561	3.382	
			beta_1	-0.116	0.160	-0.429	0.198		beta_1	-0.684	0.287	-1.246	-0.121		beta_1	0.280	0.279	-0.266	0.826	
			alpha_6	-0.884	0.109	-1.097	-0.671		Rain	-0.024	0.168	-0.354	0.306		Rain	-0.107	0.255	-0.608	0.393	
			Rainmon	0.094	0.155	-0.211	0.398		Intervention	-0.496	0.172	-0.834	-0.159		Intervention	-0.581	0.215	-1.002	-0.160	
			Rain2mon	-0.121	0.126	-0.368	0.126													
			Maxtemp	-0.208	0.127	-0.457	0.040													
			Intervention	-1.503	0.495	-2.472	-0.533													
<i>Meso-predators</i>																				
	Mammal-eating pythons	0.031*						0.029 *						0.021*						
			(Intercept)	0.796	0.506	-0.196	1.789		(Intercept)	2.382	0.256	1.881	2.883		(Intercept)	4.121	0.183	3.763	4.479	
			beta_1	-0.080	0.083	-0.243	0.083		beta_1	0.486	0.049	0.391	0.581		beta_1	-0.191	0.050	-0.289	-0.092	
			alpha_6	-0.864	0.061	-0.983	-0.744		Rain	0.334	0.051	0.234	0.435		Rain	-0.294	0.117	-0.523	-0.065	
			Rainmon	0.128	0.038	0.054	0.203		Intervention	0.736	0.077	0.585	0.888		Intervention	1.324	0.098	1.133	1.515	
			Rain2mon	0.036	0.020	-0.004	0.075													
			Maxtemp	-0.049	0.014	-0.076	-0.021													
			Intervention	0.894	0.319	0.269	1.518													
	Skink-eating elapids	< 0.001***						0.006 **						0.024*						
			(Intercept)	0.007	0.234	-0.452	0.466		(Intercept)	1.308	0.378	0.567	2.050		(Intercept)	1.898	0.217	1.473	2.324	
			beta_1	0.741	0.484	-0.208	1.690		beta_1	0.075	0.099	-0.118	0.269		beta_1	0.028	0.096	-0.160	0.216	
			alpha_6	0.240	0.255	-0.261	0.740		Rain	0.719	0.173	0.380	1.058		Rain	-1.065	0.188	-1.433	-0.696	
			Rainmon	0.018	0.137	-0.251	0.286		Intervention	1.761	0.308	1.157	2.366		Intervention	1.170	0.302	0.578	1.761	
			Rain2mon	0.177	0.071	0.038	0.315													
			Maxtemp	-0.074	0.028	-0.128	-0.019													
			Intervention	1.127	0.597	-0.042	2.297													
	Colubrids	0.018*						0.017 *						0.023*						
			(Intercept)	-0.512	0.232	-0.967	-0.057		(Intercept)	2.338	0.2233	1.9	2.775		(Intercept)	3.608	0.312	2.997	4.220	
			beta_1	-0.416	0.232	-0.871	0.039		beta_1	0.422	0.0465	0.331	0.513		beta_1	-0.181	0.104	-0.385	0.023	
			alpha_6	0.567	0.189	0.196	0.937		Rain	0.004	0.0708	-0.135	0.143		Rain	0.158	0.149	-0.135	0.450	
			Rainmon	-0.155	0.235	-0.616	0.307		Intervention	0.775	0.1122	0.555	0.995		Intervention	1.013	0.156	0.708	1.318	
			Rain2mon	0.388	0.218	-0.039	0.814													
			Maxtemp	-0.397	0.216	-0.821	0.026													
			Intervention	0.573	0.206	0.168	0.977													
	Frogs + agamids + large skinks	0.002**						NA						NA						
			(Intercept)	1.568	0.2727	1.0337	2.1025													
			beta_1	-0.148	0.0934	-0.3306	0.0354													
			alpha_6	0.176	0.1298	-0.0783	0.4306													
			Rainmon	0.329	0.16	0.0154	0.6427													
			Rain2mon	-0.193	0.1894	-0.5639	0.1784													
			Maxtemp	0.414	0.2182	-0.0139	0.8413													

Vegcov	0.38	0.1591	0.6926	0.068
Mthsincefire	-0.394	0.1297	-0.6479	-0.1394
Intervention	1.204	0.2067	0.7988	1.6089

Prey

Small mammals	0.004**				NA	NA
(Intercept)		0.0694	0.3972	-0.7091	0.848	
beta_1		0.4546	0.0728	0.312	0.597	
alpha_6		0.5236	0.1078	0.3123	0.735	
Rainmon		0.3961	0.1328	0.1359	0.656	
Rain2mon		1.8181	0.201	1.4243	2.212	
Maxtemp		0.2302	0.097	0.0401	0.42	
Vegcov		0.5107	0.1852	0.1477	0.874	
Mthsincefire		1.671	0.1973	1.2843	2.058	
Intervention		-0.4952	0.1146	-0.7199	-0.271	
Small skinks + herbivorous invertebrates	0.008**				NA	NA
(Intercept)		3.7939	1.12	1.599	5.9892	
beta_1		-0.0948	0.133	-0.355	0.1655	
alpha_12		-0.4484	0.452	-1.334	0.4368	
Rainmon		-0.5768	0.244	-1.055	-0.0989	
Rain2mon		-0.2592	0.215	-0.68	0.1618	
Maxtemp		0.1146	0.137	-0.154	0.383	
Vegcov		-0.3628	0.176	-0.708	-0.0178	
Mthsincefire		-0.1122	0.178	-0.461	0.2368	
Intervention		-1.3623	0.256	-1.864	-0.8603	
Carnivorous invertebrates	0.356				NA	NA
(Intercept)		3.6451	0.681	2.3096	4.9806	
beta_1		0.2222	0.13	-0.0335	0.478	
alpha_12		-0.7963	0.267	-1.3202	-0.2725	
Rainmon		0.4287	0.151	0.1329	0.7245	
Rain2mon		0.1868	0.168	-0.1421	0.5157	
Maxtemp		0.5041	0.186	0.1405	0.8678	
Vegcov		-0.1587	0.12	-0.3936	0.0763	
Mthsincefire		-0.0675	0.136	-0.3331	0.1981	
Intervention		-0.4245	0.191	-0.7996	-0.0494	

Significance codes . 0.1, * 0.05, ** 0.01, *** 0.001

Table S2. Snake, reptile and mammal species represented in callout and survey records from Kununurra (KNX, Mirima), Katherine (KAT) and Darwin (DAR). Fauna species and taxa are grouped according to predatory hierarchy (apex- and meso-predators and prey) and functional groupings within the conceptual model (see Fig. X). Numbers in bold are those for which intervention analyses were undertaken. Dietary information for reptile and frog species/genera was taken from Cogger (2014) and from Menkhorst and Knight (2011) for small mammals. Size of each species is the mean length of animals captured during wildlife removals/surveys, or if not measured, maximum length as recorded in Cogger (2014). *Denotes the number of introduced cane toads collected at Kununurra drop-off points from April 2010 through to the end of 2013.

Functional group	Species	Common name	SVL (cm)	Diet	KNX	KAT	DAR	Mirima (KNX)
APEX PREDATORS								
Large-bodied/gaped elapids	<i>Pseudechis australis</i>	King brown, mulga	139	reptiles including snakes, frogs, small mammals	20	38	28	7
	<i>Pseudonaja nuchalis</i>	Western brown, gwardar	106	reptiles, small mammals, frogs	28	68	144	7
	<i>Pseudonaja ingrami</i>	Ingram's brown	100	vertebrates	-	1	-	-
	<i>Pseudonaja textilis</i>	Eastern brown	200	small mammals, reptiles	-	1	-	-
	<i>Pseudechis weigeli</i>	Pygmy, speckled mulga	120	vertebrates	-	21	-	1
Varanids	<i>Varanus gouldii</i>	Sand monitor, Gould's monitor	113	reptiles, insects, birds, mammals, frogs, carrion	6	-	-	16
	<i>Varanus acanthurus</i>	Spiny tailed monitor	70	lizards, insects	-	-	-	6
	<i>Varanus mertensii</i>	Merten's water monitor	65	fish, frogs, carrion	4	-	-	-
	<i>Varanus mitchellii</i>	Mitchell's water monitor	35	insects, fish, frogs	-	-	-	1
	<i>Varanus scalaris</i>	Spotted tree monitor	60	insects, lizards	-	-	-	1
	<i>Varanus tristis</i>	Black headed monitor	60	arboreal reptiles, insects	-	-	-	2
	All varinids	goannas, monitors	81	reptiles, insects, birds, mammals, frogs, carrion	10	-	6	26
MESO-PREDATORS								
Pythonids	<i>Antaresia childreni</i>	Childrens python	60	small mammals, birds, reptiles	48	295	720	2
	<i>Aspidites melanocephalus</i>	Black headed python	128	small mammals, ground birds, reptiles, venomous snakes	12	49	27	-
	<i>Liasis fuscus</i>	Water python	141	small mammals, other vertebrates	24	51	637	-
	<i>Liasis olivaceous</i>	Olive python	160	small mammals, other vertebrates	71	266	237	-
	<i>Morelia spilota</i>	Carpet python	162	small mammals, terrestrial vertebrates	-	-	993	-
Colubrids	<i>Boiga irregularis</i>	Night tiger, brown tree snake	98	small mammal, birds, eggs, lizards	5	183	297	-
	<i>Dendrelaphis punctulatus</i>	Common tree snake	112	semi-arboreal frogs, birds	74	168	1094	-
	<i>Stegonotus cucullatus</i>	Slatey grey snake	94	lizards, small mammals	-	-	668	-
	<i>Tropidonophis mairii</i>	keelback	52	frogs, semi-aquatic	6	59	117	1
Small-bodied/gaped Elapids	<i>Acanthophis rugosus</i>	Northern death adder	70	lizards, small mammals	-	-	1	1
	<i>Brachyuropsis roperi</i>	Northern shovel-nosed snake	25	reptile eggs	-	1	-	11
	<i>Cryptophis pallidiceps</i>	Secretive snake, small eyed snake	50	lizards, frogs	-	21	54	-
	<i>Demansia olivacea</i>	Olive whip snake	73	lizards	-	6	9	1
	<i>Demansia papuensis</i>	Greater black whip snake	97	lizards	21	100	71	2
	<i>Demansia simplex</i>	Grey whip snake	60	lizards	-	1	3	-
	<i>Demansia vestigiata</i>	Lesser black whip snake	160	lizards	-	63	-	-
	<i>Furina ornata</i>	Orange-naped, moonsnake	36	small skinks	9	30	-	-
	<i>Suta punctata</i>	Spotted snake	38	lizards	-	5	-	3
	<i>Vermicella</i> spp.	Bandy bandy	50	blind snakes	-	2	-	-
Acrochordids	<i>Acrochordus arafurae</i>	Arafura file snake	150	fish	-	2	2	-
Typhlopids	<i>Ramphotyphlops</i> spp.	Blind snakes	30	ants, termites	-	-	1	2
Homalopsids	<i>Fordonia leucobalia</i>	Crab eating snake	100	small fish, crabs	-	-	3	-
Agamids	<i>Chelosania brunnea</i>	Chameleon dragon	22	invertebrates	-	-	-	3

	<i>Diporiphora inungui</i>	Yellow-eyed two-lined dragon	25	invertebrates	-	-	-	92
	<i>Diporiphora pindan</i>	Pindan two-lined dragon	17	invertebrates	-	-	-	61
	<i>Lophognathus gilberti</i>	Gilberts dragon	38	invertebrates	-	-	-	14
	All Diporiphora							153
Large Scincids	<i>Ctenotus inornatus</i>	Bar-shouldered ctenotus	19	invertebrates	-	-	-	123
	<i>Ctenotus pantherinus</i>	Leopard ctenotus	27	invertebrates	-	-	-	1
	<i>Ctenotus piankai</i>	Pianka's ctenotus	19	invertebrates	-	-	-	5
	<i>Ctenotus robustus</i>	Robust ctenotus	24	invertebrates	-	-	-	248
	<i>Ctenotus tantillus</i>	Kimberley wedge snout ctenotus	18	invertebrates	-	-	-	2
	All Ctenotus							379
	<i>Eremiascincus isolepis</i>	Northern bar-lipped skink	13	invertebrates				94
Gekkonids	<i>Heteronotia binoei</i>	Binoe's gecko	9	invertebrates				107
Anurans	<i>Crinia biligua</i>	Bilingual froglet	4	invertebrates	-	-	-	18
	<i>Cyclorana</i> spp.	Large terrestrial frogs	5	invertebrates	-	-	-	40
	<i>Litoria</i> spp.	Tree frogs	4	invertebrates	-	-	-	22
	<i>Lymnodynastes convexiusculus</i>	Marbled frog	4	invertebrates	-	-	-	13
	<i>Notadon melanoscapus</i>	Northern spadefoot frog	4	invertebrates	-	-	-	9
	<i>Platyplectrum ornatum</i>	Ornate frog	3	invertebrates	-	-	-	266
	<i>Uperoleia</i> spp.	toadlets	2	invertebrates	-	-	-	131
	All frogs							487
	<i>Rhinella marina</i>	Cane toad	5	invertebrates	22623*	-	-	205
PREY								
Rodents	<i>Pseudomys delicatulus</i>	Delicate mouse	14	seeds, plant matter, insects	-	-	-	59
	<i>Pseudomys nanus</i>	Western chestnut mouse	26	grass stems	-	-	-	10
	<i>Rattus tunneyi</i>	Pale field rat	34	vegetation	-	-	-	22
	<i>Zyzomys argurus</i>	Common rock rat	24	seeds, plant matter, insects	-	-	-	8
Small Dasyurids	<i>Planigale ingrami</i>	Long tailed planigale	12	invertebrates, small vertebrates	-	-	-	5
	All small mammals				-	-	-	104
Small Scincids	<i>Carlia</i> spp.	Rainbow skinks	11	small invertebrates	-	-	-	234
	<i>Lerista griffini</i>	Stout sandslider	9	ants, termites	-	-	-	269
	<i>Menetia greyii</i>	Dwarf skink	6	small invertebrates	-	-	-	6
	<i>Morethia ruficauda</i>	Fire-tail skink	8	small invertebrates	-	-	-	57
	<i>Notoscincus ornatus</i>	Ornate skink	7	small invertebrates	-	-	-	31
	<i>Proablepharus tenuis</i>	Northern soil crevice skink	6	small invertebrates	-	-	-	2
	Tiny skinks (< 8 cm)							96
Large invertebrates	Carnivorous invertebrates				-	-	-	806
	Herbivorous invertebrates				-	-	-	415
	Carabidae	Carabid beetles	3	invertebrates, small vertebrates	-	-	-	379
	Chilopoda	Centipedes	12	invertebrates, small vertebrates	-	-	-	318
	Blattodea	Cockroaches	2	detritus, plant material	-	-	-	254
	Gryllidae	Crickets	2	plant material	-	-	-	68
	Scorpiones	Scorpions	5	invertebrates	-	-	-	44
	Araneae	Spiders	2	invertebrates	-	-	-	61
	All invertebrates							1221

Table S3. Covariates used in modelling of time series generalised linear models (INBARC) log-linear models with logarithmic link). Italics indicate name used in reporting of modelling results (Table 1, Table S3). All continuous variables were centred and standardised by dividing by two times the standard deviation [76].

Parameter	Coding	Comment
<i>beta_1</i>	As defined in R package tscount [53]	1 st order autoregressive term on previous observation in time series
<i>alpha_6, alpha_12</i>	As defined in R package tscount [53]	6 th or 12 th order autoregressive term on 6-monthly or 12-monthly (respectively) previous mean in time series
Intervention	As defined in R package tscount [53]	Intervention covariate for month of cane toad invasion in (1) Kununurra, May 2010; (2) Darwin, 2005; (3) Mirima, April 2011; (4) Katherine, 2001; (5) Katherine, 2005
Maximum temperature (<i>maxtemp</i>)	Continuous, centred, standardised	Mean maximum temperature (°C), monthly for Kununurra or Mirima, yearly for Darwin or Katherine
Monthly rainfall (<i>rainmon</i>)	Continuous, centred, standardised	Mean monthly rainfall (mm) for Kununurra or Mirima
Two-monthly rainfall (<i>rain2mon</i>)	Continuous, centred, standardised	Mean rainfall over previous two months (mm) for Kununurra or Mirima
Annual rainfall (<i>rain</i>)	Continuous, centred, standardised	Mean annual rainfall (mm) for Darwin or Katherine
Time since fire (<i>mthsincefire</i>)	Integer, standardised	Number of months since last fire, included as covariate in Mirima models
Vegetation cover (<i>vegcov</i>)	Integer, standardised	Percentage cover of sub-canopy shrub and herbaceous vegetation, included as covariate in Mirima models

Table S4. Time series generalised linear models (GLM) and generalised additive models with logarithmic link (from occurrence records of species/functional/trophic groups of apex, meso-predators and prey trophic levels at different sites. Model coefficient estimates, standard error (SE) and 95% confidence intervals (CI) are shown. Intervention effect at the time of cane toad invasion (and/or at a lagged time after cane toad invasion) is indicated as significantly negative (↓), significantly positive (↑), or non-significant (NS) and the time of intervention effect is given. For definitions of variables see Table S2.

Study site	Trophic group	Functional group/species	Coefficients	Estimate	SE	CI		Intervention effect	
						Lower	Upper	At cane toad invasion	At lagged time
Kununurra									
	Apex predators								
		Anurophagous, snake-eating:							
		<i>Pseudechis australis</i>	(Intercept)	-3.431	0.601	-4.608	-2.253	↓ May 2010	
			beta_1	0.375	0.223	-0.062	0.812		
			alpha_12	-1.000	0.199	-1.390	-0.610		
			Intervention	-1.084	0.606	-2.272	0.104		
		<i>Pseudonaja nuchalis</i>	(Intercept)	-0.244	0.726	-1.667	1.178	↓ May 2010	
			beta_1	0.248	0.237	-0.216	0.712		
			alpha_12	0.671	0.420	-0.153	1.494		
			Maxtemp	-0.255	0.272	-0.789	0.279		
			Intervention	-0.454	0.265	-0.973	0.064		
		<i>Varanus spp.</i>	(Intercept)	-3.995	0.805	-5.571	-2.418	↓ May 2010	↓ April 2011 (Mirima)
			beta_1	-0.087	0.458	-0.985	0.811		
			alpha_6	-0.913	0.105	-1.119	-0.706		
			Maxtemp	-0.308	0.198	-0.696	0.080		
			Intervention	-3.034	1.382	-5.742	-0.326		
	Meso-predators								
		Mammal-eating pythons:							
		<i>Antaresia childreni</i>	(Intercept)	-0.857	0.542	-1.920	0.206	↑ May 2010	
			beta_1	-0.060	0.246	-0.542	0.421		
			alpha_12	0.467	0.315	-0.151	1.084		
			Rainmon	0.477	0.238	0.010	0.944		
			Intervention	0.465	0.324	-0.170	1.100		
		<i>Aspidites melanocephalus</i>	(Intercept)	-8.407	1.693	11.725	-5.089	↑ May 2010	
			beta_1	0.348	0.311	-0.260	0.957		
			alpha_6	-1.000	0.089	-1.174	-0.826		
			Rainmon	0.461	0.269	-0.066	0.988		
			Intervention	1.889	1.534	-1.117	4.895		
		<i>Liasis fuscus</i>	(Intercept)	-1.051	0.536	-2.103	0.000	↑ May 2010	
			beta_1	-0.342	0.327	-0.983	0.298		
			alpha_12	0.784	0.126	0.538	1.030		
			Rain2mon	0.569	0.242	0.094	1.044		
			Maxtemp	-0.528	0.246	-1.010	-0.047		
			Intervention	0.936	0.446	0.061	1.811		
		<i>Liasis olivaceus</i>	(Intercept)	-0.167	0.162	-0.485	0.150	↑ May 2010	
			beta_1	0.124	0.102	-0.076	0.324		
			alpha_12	0.760	0.173	0.422	1.098		

			Intervention	0.325	0.153	0.026	0.625		
	Skink-eating elapids:								
	<i>Demansia papuensis</i>	(Intercept)	-1.088	0.537	-2.141	-0.036		↑ May 2010	
		beta_1	-0.030	0.222	-0.466	0.406			
		alpha_6	0.627	0.179	0.277	0.977			
		Rain2mon	0.374	0.305	-0.224	0.971			
		Maxtemp	-0.846	0.428	-1.685	-0.008			
		Intervention	1.514	0.358	0.812	2.216			
	<i>Furina ornata</i>	(Intercept)	-8.525	1.776	12.006	-5.043		↑ May 2010	
		beta_1	0.437	0.301	-0.154	1.027			
		alpha_6	-0.946	0.117	-1.175	-0.716			
		Rainmon	0.370	0.182	0.014	0.726			
		Intervention	3.323	1.382	0.613	6.032			
	Arboreal colubrids:								
	<i>Dendrelaphis punctulatus</i>	(Intercept)	-1.041	0.243	-1.516	-0.566		↑ May 2010	
		beta_1	-0.263	0.279	-0.810	0.284			
		Maxtemp	-0.382	0.238	-0.849	0.085			
		Intervention	0.723	0.280	0.174	1.271			
	<i>Boiga irregularis</i>	(Intercept)	-9.663	1.676	12.947	-6.379		↑ May 2010	
		beta_1	0.859	0.108	0.648	1.071			
		alpha_6	-0.822	0.098	-1.013	-0.631			
		Intervention	2.507	1.265	0.026	4.987			
	<i>Tropidonophis mairii</i>	(Intercept)	-7.878	1.622	11.057	-4.700		↑ May 2010	
		beta_1	-0.009	0.246	-0.491	0.472			
		alpha_6	-0.991	0.141	-1.267	-0.714			
		Rain2mon	0.043	0.128	-0.208	0.295			
		Intervention	1.854	1.430	-0.949	4.657			
	Frogs:								
	<i>Uperoleia</i>	(Intercept)	-0.896	0.428	-1.735	-0.058		NS April 2010	↑ April 2011
		beta_1	-1.000	0.382	-1.749	-0.251			
		Rainmon	1.741	0.467	0.825	2.657			
		Vegcov	0.730	0.341	0.062	1.397			
		Intervention	1.705	0.496	0.734	2.677			
	<i>Platyplectrum ornatum</i>	(Intercept)	-1.310	0.459	-2.210	-0.406		NS April 2010	↑ April 2011
		Vegcov	-2.360	0.616	-3.570	-1.153			
		Mthsincefire	-1.060	0.364	-1.770	-0.349			
		Intervention	1.780	0.443	0.910	2.644			
	Agamids	(Intercept)	-0.458	0.463	-1.365	0.449		↑ April 2010	↑ April 2011
		beta_1	0.304	0.269	-0.223	0.830			

			Intervention	0.788	0.493	-0.179	1.755		
	Large skinks:								
	Large <i>Ctenotus</i> spp.	(Intercept)	0.283	0.251	-0.209	0.776	NS April 2010	↑ April 2011	
		Maxtemp	0.521	0.313	-0.093	1.135			
		Vegcov	-0.831	0.295	-1.410	-0.253			
		Intervention	1.105	0.303	0.511	1.699			
	<i>Eremiascincus isolepis</i>	(Intercept)	0.001	0.654	-1.281	1.283	NS April 2010	NS April 2011	
		beta_1	-0.264	0.385	-1.018	0.491			
		alpha_12	-0.625	0.446	-1.499	0.249			
		Rainmon	0.916	0.496	-0.056	1.889			
		Maxtemp	1.149	0.627	-0.080	2.378			
		Intervention	-0.230	0.488	-1.187	0.727			
	<i>Heteronotia binoei</i>	(Intercept)	-0.729	0.590	-1.886	0.427	NS April 2010	NS April 2011	
		beta_1	0.131	0.244	-0.346	0.609			
		alpha_12	-0.469	0.363	-1.180	0.242			
		Rainmon	-1.128	0.495	-2.098	-0.159			
		Maxtemp	-0.685	0.357	-1.385	0.015			
		Vegcov	0.626	0.399	-0.155	1.408			
		Intervention	0.818	0.479	-0.120	1.756			
	Crocodile:								
	<i>Crocodylus johnsoni</i>	(Intercept)	-3.319	0.712	-4.713	-1.920	↑ May 2010	↑ April 2011	
		Rainmon	0.787	0.331	0.139	1.440			
		Intervention	1.507	0.753	0.031	2.980			
Prey									
	<i>Lerista griffini</i>	(Intercept)	0.778	0.317	0.157	1.399	↓ April 2010	↓ April 2011	
		Rainmon	-1.937	0.733	-3.374	-0.501			
		Rain2mon	-1.127	0.601	-2.304	0.051			
		Vegcov	0.638	0.337	-0.023	1.299			
		Intervention	-0.909	0.290	-1.478	-0.340			
	<i>Carlia</i> spp.	(Intercept)	-2.553	0.822	-4.163	-0.942	↑ April 2010	↑ April 2011	
		beta_1	-0.214	0.295	-0.792	0.363			
		alpha_12	-0.786	0.365	-1.500	-0.071			
		Rainmon	-0.912	0.559	-2.007	0.184			
		Mthsincefire	-1.028	0.476	-1.960	-0.095			
		Intervention	2.380	0.650	1.106	3.653			
	Tiny skinks (<i>Menetia</i> , <i>Morethia</i> , <i>Notoscincus</i> spp.)	(Intercept)	-0.199	0.519	-1.220	0.819	↓ April 2010	↓ April 2011	
		alpha_12	-0.642	0.448	-1.520	0.236			
		Rainmon	-1.489	0.766	-2.990	0.011			
		Intervention	-0.998	0.561	-2.100	0.103			
Darwin									
	Apex predators								
	Anurophagous, snake-eating:								

			(Intercept)	1.722	0.214	1.300	2.141	↓ 2005	
			Rain	-0.528	0.391	-1.300	0.239		
			Intervention	-1.604	0.463	-2.510	-0.697		
		<i>Pseudonaja nuchalis</i>	(Intercept)	2.963	0.148	2.672	3.254	↓ 2005	
			Rain	0.093	0.205	-0.309	0.496		
			Intervention	-0.309	0.199	-0.699	0.082		
	Meso-predators								
		Mammal-eating pythons:							
		<i>Antaresia childreni</i>	(Intercept)	6.800	1.230	4.389	9.212	↑ 2005	
			beta_1	-0.658	0.301	-1.248	-0.068		
			Rain	-0.113	0.096	-0.302	0.075		
			Intervention	0.716	0.149	0.424	1.007		
		<i>Aspidites melanocephalus</i>	(Intercept)	0.198	0.452	-0.688	1.080	↑ 2005	
			Rain	0.192	0.431	-0.653	1.040		
			Intervention	1.296	0.503	0.310	2.280		
		<i>Liasis fuscus</i>	(Intercept)	6.642	0.687	5.296	7.988	↑ 2005	
			beta_1	-0.800	0.191	-1.174	-0.427		
			Rain	-0.124	0.093	-0.306	0.059		
			Intervention	1.375	0.172	1.038	1.713		
		<i>Liasis olivaceus</i>	(Intercept)	2.895	0.119	2.662	3.127	↑ 2005	
			Rain	-0.047	0.147	-0.335	0.241		
			Intervention	0.598	0.144	0.316	0.879		
		<i>Morelia spilota</i>	(Intercept)	5.427	0.577	4.296	6.558	↑ 2005	
			beta_1	-0.447	0.159	-0.760	-0.135		
			Rain	-0.346	0.119	-0.579	-0.113		
			Intervention	1.848	0.224	1.409	2.287		
		Skink-eating elapids:							
		<i>Cryptophis pallidiceps</i>	(Intercept)	1.174	0.280	0.626	1.720	↑ 2005	
			Rain	0.045	0.308	-0.559	0.650		
			Intervention	0.934	0.324	0.299	1.570		
		<i>Demansia papuensis</i>	(Intercept)	1.604	0.226	1.162	2.050	↑ 2005	
			Rain	0.049	0.266	-0.473	0.570		
			Intervention	0.722	0.269	0.195	1.250		
		<i>Furina ornata</i>	(Intercept)	2.111	0.478	1.174	3.047	↑ 2005	
			beta_1	-0.855	0.334	-1.509	-0.201		
			Rain	0.010	0.346	-0.669	0.689		
			Intervention	1.664	0.408	0.864	2.463		
		Arboreal colubrids:							
		<i>Dendrelaphis punctulatus</i>	(Intercept)	4.265	0.060	4.147	4.382	↑ 2005	
			Rain	-0.378	0.074	-0.523	-0.232		

			Intervention	0.783	0.070	0.645	0.920		
		<i>Boiga irregularis</i>	(Intercept)	2.637	0.135	2.373	2.902	↑ 2005	
			Rain	-0.221	0.141	-0.498	0.055		
			Intervention	1.220	0.151	0.924	1.516		
		<i>Tropidonophis mairii</i>	(Intercept)	0.765	0.336	0.107	1.422	↑ 2005	
			Rain	0.316	0.207	-0.090	0.721		
			Intervention	2.326	0.350	1.640	3.011		
		<i>Stegonotus cucullatus</i>	(Intercept)	4.666	0.457	3.770	5.562	↑ 2005	
			beta_1	-0.696	0.184	-1.060	-0.334		
			Rain	-0.705	0.196	-1.090	-0.322		
			Intervention	3.207	0.399	2.430	3.988		
Katherine									
	Apex predators								
		Anurophagous, snake-eating:							
		<i>Pseudechis australis</i>	(Intercept)	0.239	1.144	-2.004	2.482	↓ 2001	
			beta_1	0.838	0.589	-0.317	1.994		
			Rain	-0.827	0.516	-1.839	0.184		
			Intervention	-2.310	1.266	-4.791	0.170		
		<i>Pseudonaja nuchalis</i>	(Intercept)	2.869	0.655	1.590	4.153	↓ 2001	
			beta_1	-0.376	0.335	-1.030	0.281		
			Intervention	-0.515	0.250	-1.010	-0.025		
	Meso-predators								
		Mammal-eating pythons:							
		<i>Antaresia childreni</i>	(Intercept)	3.438	0.200	3.046	3.830	↑ 2001	↑ 2005
			beta_1	-0.283	0.073	-0.426	-0.141		
			Rain	-0.813	0.147	-1.101	-0.526		
			Intervention	1.130	0.143	0.850	1.411		
		<i>Aspidites melanocephalus</i>	(Intercept)	0.219	0.404	-0.573	1.011	↑ 2001	↑ 2005
			beta_1	-0.591	0.145	-0.876	-0.306		
			Rain	-2.641	0.685	-3.983	-1.298		
			Intervention	2.348	0.420	1.525	3.171		
		<i>Liasis fuscus</i>	(Intercept)	1.047	0.377	0.308	1.786	↑ 2001	↑ 2005
			beta_1	-0.333	0.292	-0.906	0.239		
			Intervention	1.553	0.404	0.760	2.346		
		<i>Liasis olivaceus</i>	(Intercept)	2.090	0.186	1.724	2.454	↑ 2001	↑ 2005
			Rain	-1.090	0.164	-1.413	-0.768		
			Intervention	1.230	0.192	0.855	1.607		
		Skink-eating elapids:							
		<i>Cryptophis pallidiceps</i>	(Intercept)	-1.838	1.004	-3.810	0.129	NS 2001	↑ 2005
			Rain	-0.794	0.584	-1.940	0.352		

			3.135	1.025	1.130	5.143		
	<i>Demansia papuensis</i>	(Intercept)	-2.316	1.023	-4.321	-0.312	↑ 2001	↑ 2005
		beta_1	-0.175	0.088	-0.346	-0.003		
		Rain	-2.506	0.570	-3.622	-1.390		
		Intervention	5.226	1.036	3.196	7.255		
	<i>Demansia vestigiata</i>	(Intercept)	1.611	0.374	0.879	2.344	NS 2001	↓ 2005
		beta_1	0.318	0.150	0.023	0.612		
		Intervention	-2.634	0.697	-4.000	-1.267		
	<i>Furina ornata</i>	(Intercept)	0.030	0.396	-0.747	0.807	↑ 2001	↑ 2005
		Rain	-1.215	0.531	-2.256	-0.173		
		Intervention	1.320	0.432	0.474	2.166		
	<i>Pseudechis weigeli</i>	(Intercept)	-0.025	0.370	-0.751	0.700	↑ 2001	↑ 2005
		Rain	-1.146	0.725	-2.568	0.276		
		Intervention	1.118	0.470	0.197	2.038		
	Arboreal colubrids:							
	<i>Dendrelaphis punctulatus</i>	(Intercept)	1.580	0.298	0.996	2.164	↑ 2001	↑ 2005
		beta_1	-0.602	0.247	-1.085	-0.118		
		Rain	-0.476	0.200	-0.868	-0.084		
		Intervention	3.168	0.722	1.752	4.584		
	<i>Boiga irregularis</i>	(Intercept)	3.257	0.341	2.590	3.925	↑ 2001	↑ 2005
		beta_1	-0.381	0.144	-0.664	-0.098		
		Rain	-0.617	0.173	-0.955	-0.278		
		Intervention	0.977	0.188	0.609	1.345		
	<i>Tropidonophis mairii</i>	(Intercept)	0.669	0.288	0.104	1.233	↑ 2001	↑ 2005
		Rain	-1.123	0.370	-1.848	-0.398		
		Intervention	1.395	0.314	0.779	2.010		

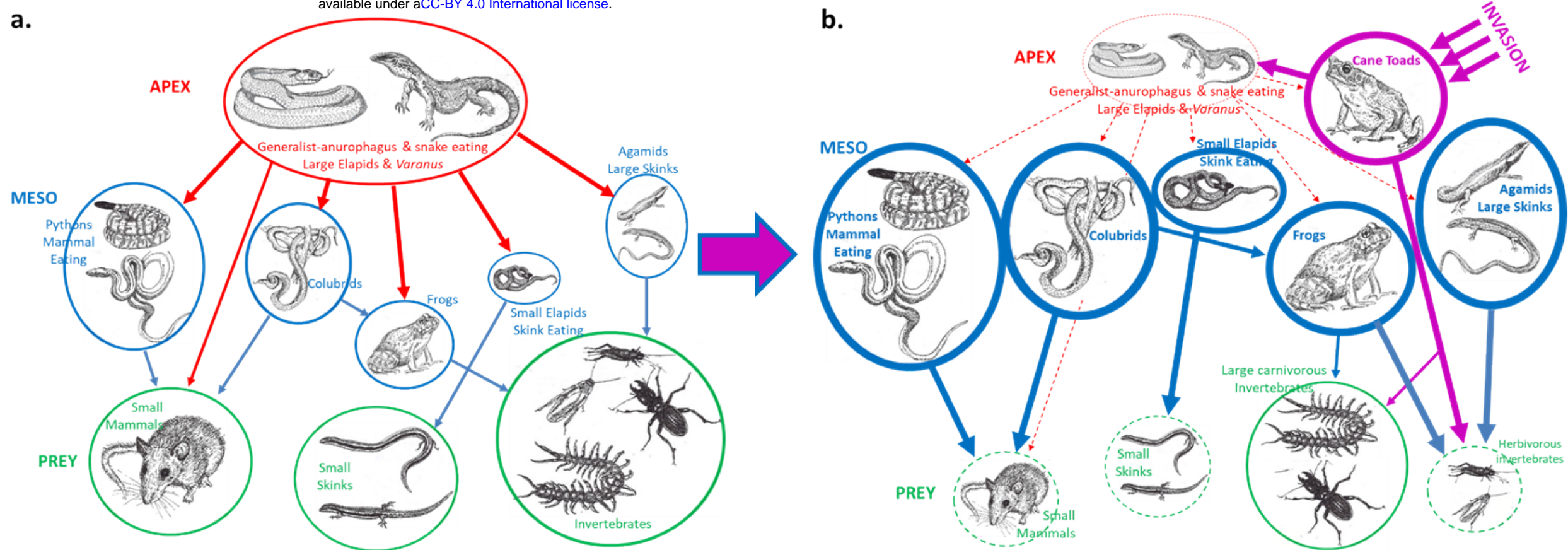


Fig. 1. A conceptual model predicting changes in trophic interactions among terrestrial savanna fauna with the arrival of cane toads (*Rhinella marina*) in savannas adjacent to Kununurra. Savanna apex reptilian predators include large elapid snakes (e.g. *Pseudechis australis*) and varanid lizards (*Varanus gouldii*). Meso-predatory reptiles include mammal-eating snakes such as pythons (e.g. *Aspidites melanocephalus* and *Liasis olivaceus*), colubrid snakes (e.g. *Dendrelaphus punctulatus*) and small skink-eating elapids (e.g. *Furina ornata*). Other savanna meso-predators include frogs (e.g. *Platyplectrum ornatum*), large scincids (e.g. *Ctenotus robustus*) and agamids (*Lophognathus gilberti*). Arrow thickness represents the strength of the interactions between trophic levels (apex and meso-predators and prey species). Thin, dashed lines or arrows indicate putative declines or weakened interactions. Violet arrows/lines represent interactions with the invasive cane toad, red lines/arrows represent apex predators and their interactions, blue lines/arrows meso-predators and their interactions, and green lines are key savanna prey species/groups. **a)** Represents a conceptual model of trophic interactions in savanna ecosystems prior to cane toad invasion. Pre-invasion reptilian and amphibian assemblages were dominated by the apex predators, which were the large-gaped anurophagous/generalist reptiles, which suppressed many of the meso-predatory savanna species, including reptilian, amphibian and mammal species. In this pre-invasion ecosystem, prey groups including small mammals, small skinks and invertebrates persisted at moderate abundance. **b)** Shows how these interactions are predicted to alter following cane toad invasion. With the loss of ca. 80% of the large, anurophagous/generalist apex reptilian predators, meso-predatory snakes, frogs, skinks and agamids increased by ca. 250 % and cane toads were introduced as an additional meso-predator. Under this scenario, there was increased predation pressure on prey groups including small mammals, small skinks and some invertebrates (herbivorous) which resulted in declines in these groups of ca. 30-80%. Note that large predatory invertebrates including carabid beetles and centipedes neither declined nor increased following cane toad invasion.