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**

3

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

54   savanna

INTRODUCTION

"We were the Leopards, the Lions; those who'll take our place will be little jackals, hyena -

and sheep", Giuseppe Tomasi di Lampedusa (The Leopard)

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

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

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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

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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 ºC), 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 ºC (Katherine) and 30.6–33.3

166 ºC (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

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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 cm $\times$ 60 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 (tau); in our case, tau 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 (delta (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

13

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 (alpha_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

15

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

16

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

17

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

19

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

21

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/ecy.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.

23

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, at 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.

26

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.

56. Ziembicki MR, Woinarski JC, Mackey B. Evaluating the status of species using Indigenous knowledge: Novel evidence for major native mammal declines in northern Australia. Biological Conservation. 2013;157:78-92.

57. Ibbett M, Woinarski JCZ, Oakwood M. Declines in the mammal assemblage of a rugged sandstone environment in Kakadu National Park, Northern Territory, Australia. Australian Mammalogy. 2017;doi:10.1071/AM17011.

58. Stokeld D, Fisher A, Gentles T, Hill B, Triggs B, Woinarski JCZ, Gillespie GR. What do predator diets tell us about mammal declines in Kakadu National Park? Wildlife Research. 2018;10.1071/WR17101.

59. Davies HF, McCarthy MA, Firth RSC, Woinarski JCZ, Gillespie GR, Andersen AN, et al. Declining populations in one of the last refuges for threatened mammal species in northern Australia. Austral Ecology. 2018;doi:10.1 11 1/aec.12596.

60. Palmer C, Taylor R, Burbidge AA. Recovery Plan for the Golden Bandicoot, *Isoodon auratus*, and Golden-backed Tree-rat, *Mesembriomys macrurus*, 2004-2009. Department of Infrastructure, Planning & Environment; 2003.

61. Woinarski JC, Burbidge AA, Harrison PL. The action plan for Australian mammals 2012.

62. Burbidge AA, McKenzie NL. Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. Biological conservation. 1989;50(1-4):143-98.

63. Woinarski JCZ, Murphy BP, Palmer R, Legge SM, Dickman CR, Doherty TS, et al. How many reptiles and killed by cats in Australia? Wildlife Research. 2018;45:247-266.

64. Legge S, Murphy BP, McGregor H, Woinarski JCZ, Augusteyn J, Ballard G, et al. Enumerating a continental-scale threat: How many feral cats are in Australia? Biological 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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681 **Figure legends and embedded figures**
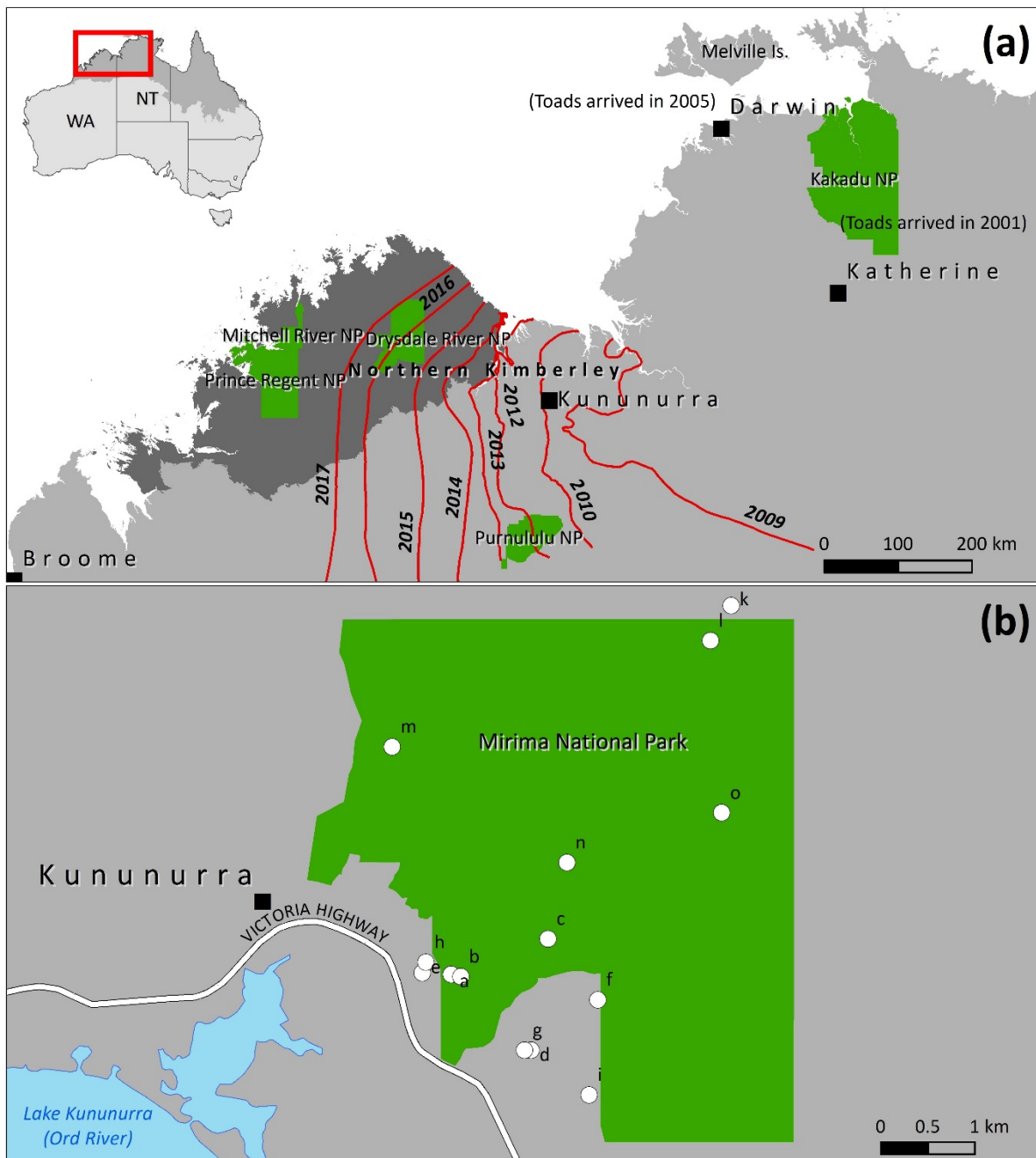
682

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

31

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.

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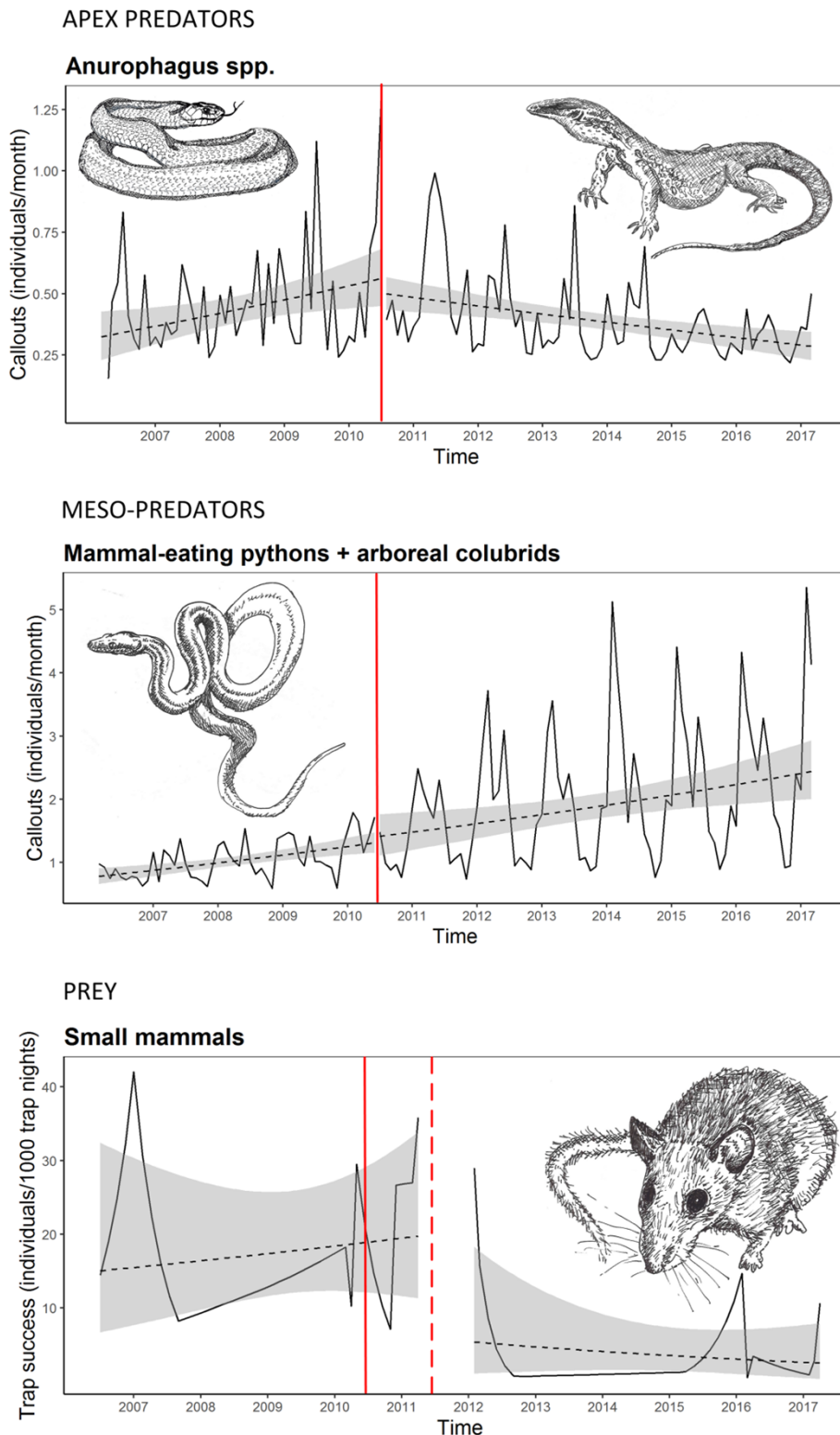
Fig. 3. Modelled trends in occurrence before and after cane toad (*Rhinella marina*) invasion for a) apex
predators (large anurophagous reptiles and elapids) from Kununurra snake callout records, b) meso-predators
(mammal-eating pythons and arboreal colubrids) from Kununurra snake callout records, and c) the small
mammal prey group from Mirima fauna surveys. The vertical solid red line indicates the arrival date of toads in
Kununurra in 2010 and the dashed red line indicates when toads arrived at fauna survey sites in 2011.
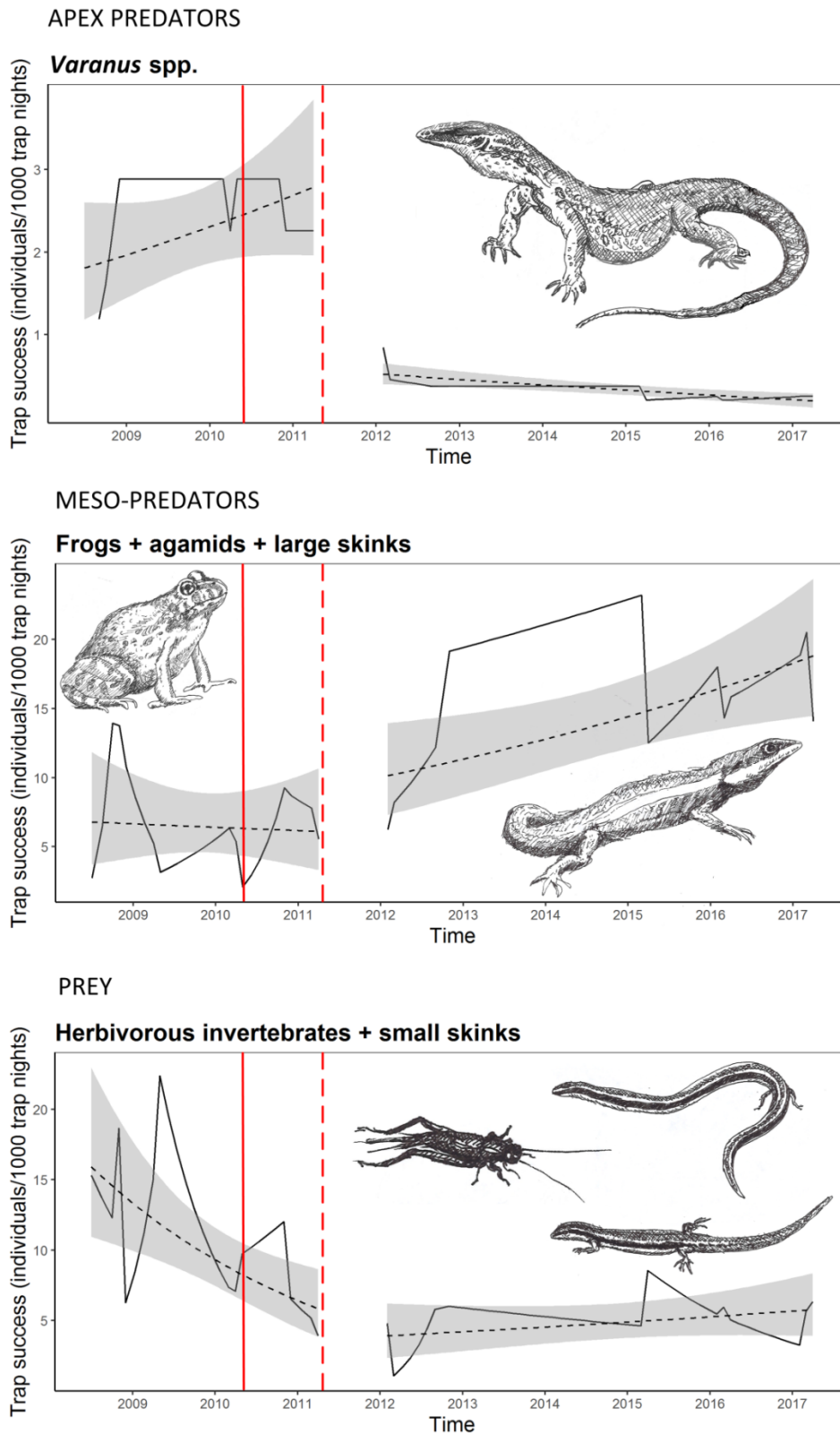
33

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

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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. [1]Denotes the first month when cane toads (*Rhinella*
712 *marina*) were recorded in drop off points in Kununurra (Intervention 1). [2]Denotes 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 20 months after the 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	Kununurra Intervention test (p-value)	Coefficients	Estimate	SE	CI (lower)	CI (upper)	Darwin Intervention test (p-value)	Coefficients	Estimate	SE	CI (lower)	CI (upper)	Katherine Intervention test (p-value)	Coefficients	Estimate	SE	CI (lower)	CI (upper)
Apex predators																			
	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												
Meso-predators																			
	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	NA						NA					
	Frogs + agamids + large skinks	0.002**																	
			(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												

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

	Diporiphora magna	? two-lined dragon	23	invertebrates	-	-	-	92
	Diporiphora pindan	Pindan two-lined dragon	17	invertebrates	-	-	-	61
	Lophognathus gilberti	Gilberts dragon	38	invertebrates	-	-	-	14
	All *Diporiphora*							**153**
Large Scincids	*Ctenotus inornatus*	Bar-shouldered ctenotus	19	invertebrates	-	-	-	123
	Ctenotus pantherinus	Leopard ctenotus	27	invertebrates	-	-	-	1
	Ctenotus piankai	Pianka's ctenotus	19	invertebrates	-	-	-	5
	Ctenotus robustus	Robust ctenotus	24	invertebrates	-	-	-	248
	Ctenotus tantillus	Kimberley wedge snout ctenotus	18	invertebrates	-	-	-	2
	All *Ctenotus*							**379**
	Eremiascincus isolepis	Northern bar-lipped skink	13	invertebrates				94
Gekkonids	*Heteronotia binoei*	Binoe's gecko	9	invertebrates				107
Anurans	*Crinia bilingua*	Bilingual froglet	4	invertebrates	-	-	-	18
	Cyclorana spp.	Large terrestrial frogs	5	invertebrates	-	-	-	40
	Litoria spp.	Tree frogs	4	invertebrates	-	-	-	22
	Lymnodynastes convexiusculus	Marbled frog	4	invertebrates	-	-	-	13
	Notadon melanoscaphus	Northern spadefoot frog	4	invertebrates	-	-	-	9
	Platyplectrum ornatum	Ornate frog	3	invertebrates	-	-	-	266
	Uperoleia spp.	toadlets	2	invertebrates	-	-	-	131
	All frogs							**487**
	Rhinella marina	Cane toad	5	invertebrates	22623*	-	-	205
PREY								
Rodents	*Pseudomys delicatulus*	Delicate mouse	14	seeds, plant matter, insects	-	-	-	59
	Pseudomys nanus	Western chestnut mouse	26	grass stems	-	-	-	10
	Rattus tunneyi	Pale field rat	34	vegetation	-	-	-	22
	Zyzomys argurus	Common rock rat	24	seeds, plant matter, insects	-	-	-	8
Small Dasyurids	*Planigale ingrami*	Long tailed planigale	12	invertebrates, small vertebrates	-	-	-	5
	All small mammals				-	-	-	**104**
Small Scincids	*Carlia* spp.	Rainbow skinks	11	small invertebrates	-	-	-	**234**
	Lerista griffini	Stout sandslider	9	ants, termites	-	-	-	**269**
	Menetia greyii	Dwarf skink	6	small invertebrates	-	-	-	**6**
	Morethia ruficauda	Fire-tail skink	8	small invertebrates	-	-	-	**57**
	Notoscincus ornatus	Ornate skink	7	small invertebrates	-	-	-	**31**
	Proablepharus tenuis	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 INGARCH 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
beta_1	As defined in R package tscount [53]	1st order autoregressive term on previous observation in time series
alpha_6, alpha_12	As defined in R package tscount [53]	6th or 12th 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 (*maxtemp*)	Continuous, centred, standardised	Mean maximum temperature (°C), monthly for Kununurra or Mirima, yearly for Darwin or Katherine
Monthly rainfall (*rainmon*)	Continuous, centred, standardised	Mean monthly rainfall (mm) for Kununurra or Mirima
Two-monthly rainfall (*rain2mon*)	Continuous, centred, standardised	Mean rainfall over previous two months (mm) for Kununurra or Mirima
Annual rainfall *(rain)*	Continuous, centred, standardised	Mean annual rainfall (mm) for Darwin or Katherine
Time since fire (*mthsincefire*)	Integer, standardised	Number of months since last fire, included as covariate in Mirima models
Vegetation cover (*vegcov*)	Integer, standardised	Percentage cover of sub-canopy shrub and herbaceous vegetation, included as covariate in Mirima models

Table S4. Time series generalised linear models (negative binomial 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 Lower	CI Upper	Intervention effect At cane toad invasion	At lagged time
Kununurra									
	Apex predators								
		Anurophagous, snake-eating:							
		Pseudechis australis	(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		
		Pseudonaja nuchalis	(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		
		Varanus spp.	(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:							
		Antaresia childreni	(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		
		Aspidites melanocephalus	(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		
		Liasis fuscus	(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		
		Liasis olivaceus	(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		

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			Intervention	0.325	0.153	0.026	0.625	
		Skink-eating elapids:						
		Demansia papuensis	(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	
		Furina ornata	(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:						
		Dendrelaphis punctulatus	(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	
		Boiga irregularis	(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	
		Tropidonophis mairii	(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:						
		Uperoliea	(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	
		Platyplectrum ornatum	(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 *Ctenotus* 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		
		Eremiascincus isolepis	(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		
		Heteronotia binoei	(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:							
		Crocodylus johnsoni	(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								
		Lerista griffini	(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		
		Carlia 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 (*Menetia, Morethia, Notoscincus* 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:							

		Pseudechis australis	(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		
		Pseudonaja nuchalis	(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:							
		Antaresia childreni	(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		
		Aspidites melanocephalus	(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		
		Liasis fuscus	(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		
		Liasis olivaceus	(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		
		Morelia spilota	(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:							
		Crytophis pallidiceps	(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		
		Demansia papuensis	(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		
		Furina ornata	(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:							
		Dendrelaphis punctulatus	(Intercept)	4.265	0.060	4.147	4.382	↑ 2005	
			Rain	-0.378	0.074	-0.523	-0.232		

				Estimate	SE	Lower	Upper		
			Intervention	0.783	0.070	0.645	0.920		
		Boiga irregularis	(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		
		Tropidonophis mairii	(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		
		Stegonotus cucullatus	(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:							
		Pseudechis australis	(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		
		Pseudonaja nuchalis	(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:							
		Antaresia childreni	(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		
		Aspidites melanocephalus	(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		
		Liasis fuscus	(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		
		Liasis olivaceus	(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:							
		Crytophis pallidiceps	(Intercept)	-1.838	1.004	-3.810	0.129	NS 2001	↑ 2005
			Rain	-0.794	0.584	-1.940	0.352		

|		Intervention	3.135	1.025	1.130	5.143		
	Demansia papuensis	(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		
	Demansia vestigiata	(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		
	Furina ornata	(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		
	Pseudechis weigeli	(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:							
	Dendrelaphis punctulatus	(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		
	Boiga irregularis	(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		
	Tropidonophis mairii	(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		

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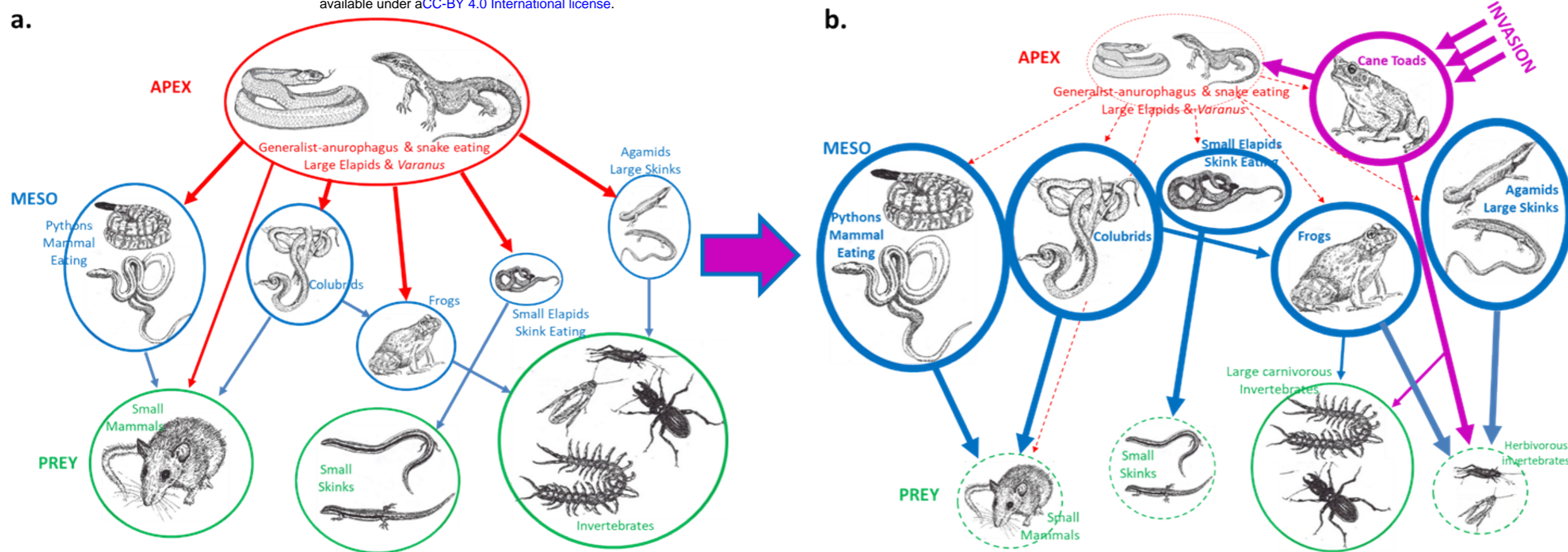
Fig. 1. A conceptual model predicting changes in trophic interactions among terrestrial savanna fauna with the arrival of cane toads (*Rhinella marina*) in savannas adjacent to Kununurra. Savanna apex reptilian predators include large elapid snakes (e.g. *Pseudechis australis*) and varanid lizards (*Varanus 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.