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A trophic cascade initiated by an invasive vertebrate alters the structure of native reptile communities

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Abstract

Invasive vertebrates are frequently reported to have catastrophic effects on the populations of species which they directly impact. It follows then, that if invaders exert strong suppressive effects on some species then other species will indirectly benefit due to ecological release from interactions with directly impacted species. However, evidence that invasive vertebrates trigger such trophic cascades and alter community structure in terrestrial ecosystems remains rare. Here, we ask how the cane toad, a vertebrate invader that is toxic to many of Australia's vertebrate predators, influences lizard assemblages in a semi-arid rangeland. In our study area, the density of cane toads is influenced by the availability of water accessible to toads. We compared an index of the abundance of sand goannas, a large predatory lizard that is susceptible to poisoning by cane toads and the abundances of four lizard families preyed upon by goannas (skinks, pygopods, agamid lizards and geckos) in areas where cane toads were common or rare. Consistent with the idea that suppression of sand goannas by cane toads initiates a trophic cascade, goanna activity was lower and small lizards were more abundant where toads were common. The hypothesis that suppression of sand goannas by cane toads triggers a trophic cascade was further supported by our findings that small terrestrial lizards that are frequently preyed upon by goannas were more affected by toad abundance than arboreal geckos, which are rarely consumed by goannas. Furthermore, the abundance of at least one genus of terrestrial skinks benefitted from allogenic ecosystem engineering by goannas where toads were rare. Overall, our study provides evidence that the invasion of ecosystems by non-native species can have important effects on the structure and integrity of native communities extending beyond their often most obvious and frequently documented direct ecological effects.

KEYWORDS
cane toad, direct effects, indirect effects, invasive species, *Rhinella marina*, semi-arid, trophic cascade, *Varanus gouldii*

1 | INTRODUCTION

The invasion of ecosystems by non-native species is a key driver of global environmental change in the Anthropocene (Vitousek, D'Antonio, Loope, Rejmanek, & Westbrooks, 1997). Over recent centuries, the frequency at which human actions facilitated the movement of species into habitat outside their natural range has markedly increased and there is no reversal of this trend in sight as our globalized economy continues to open new pathways for invaders to reach distant ecosystems (Seebens et al., 2017). The unprecedented rate of species introductions into new environments has far-reaching consequences, including the homogenization of biota (Clavel, Julliard, & Devictor, 2011), disruptions to ecosystem functioning (Sousa, Morais, Dias, & Antunes, 2011; Walsh, Carpenter, & Vander Zanden, 2016) and impacts on human well-being and the economy (Bacher et al., 2018; Pyšek & Richardson, 2010). Yet, for more than 60 years since Elton's seminal book laid foundation to the field of invasion biology (Elton, 1958), disentangling the multitude of mechanisms through which non-native species can affect ecosystems still remains one of the great challenges in modern ecology.

In contrast to the considerable attention that has been payed to the causes of invasions (Galil et al., 2016; Jeschke & Strayer, 2005; Van Kleunen, Dawson, Schlaepfer, Jeschke, & Fischer, 2010) and their immediate consequences via direct interactions with native biota (Corbin & D'Antonio, 2004; Miller & Gorchov, 2004; Risbey, Calver, Short, Bradley, & Wright, 2000; Roy et al., 2012), the potential cascading effects that invaders have on species they do not directly interact with are less well described. Nevertheless, mounting evidence indicates that invasive species have the potential to substantially alter the entire structure of native communities through cascades of indirect effects that go beyond their direct impacts on individual species (Doody et al., 2015; Feit et al., 2018; Mooney & Cleland, 2001; White, Wilson, & Clarke, 2006). Such cascades can be particularly prominent in systems where invaders affect the abundance or performance of strongly interactive keystone species such as predators, pollinators or ecosystem engineers (Anderson & Rosemond, 2007; Feit et al., 2018; Gooden, French, & Turner, 2009; Letnic, Koch, Gordon, Crowther, & Dickman, 2009). In such circumstances, invaders can propagate series of direct and indirect effects whereby shifts in the abundance of immediately affected species subsequently alter the abundance and biomass of others (Terborgh & Estes, 2010). For example, such cascades have been documented for invaders in both aquatic(e.g. Simon & Townsend, 2003; Strayer, 2010) and terrestrial ecosystems (Croll, Maron, Danner, & Byrd, 2003; Doody, Castellano, Rhind, & Green, 2013; Feit et al., 2018; Roemer, Donlan, & Courchamp, 2002).

The cane toad *Rhinella marina* is a highly successful invader that is affecting numerous keystone species across a wide range of ecosystems. Since they were first introduced from their native South and Central America to Australia in 1935, cane toads have spread over much of the continent's north (Doody et al., 2018). Like other bufonids, cane toads possess large poison glands in which they synthesize

a potent combination of toxic chemicals as a defence against predators that is not found in native Australian anurans (Lever, 2001). Because Australian carnivores have not evolved to cope with the toxins present in toads, many species are highly susceptible to fatal toxic ingestion (Phillips, Brown, & Shine, 2003; Shine, 2010). Consequently, poisoning of predators which attempt to consume cane toads has driven sharp declines in the abundances of predators such as quolls, varanid lizards, freshwater crocodiles and snakes following the toad invasion (Feit & Letnic, 2015; Shine, 2010).

Recent studies have demonstrated that this toad-induced decline of native predators can translate into increased abundances of their prey. However, a limitation of these studies is their focus on either individual prey species (Doody et al., 2006, 2009, 2013, 2015) or entire taxa (Feit et al., 2018), without investigating further consequences for the richness and composition of native species communities that might arise from differences in the strength of indirect effects initiated by the toad-induced predator decline. Such differences can occur when predators favour certain prey over others. Under these circumstances, the magnitude of predatory release is likely to vary between prey groups. Here, we addressed this question by investigating the effects of cane toads on the structure and composition of small lizard communities following a decline in varanid lizard populations in semi-arid regions of their range.

The establishment of high-density populations of cane toads in semi-arid ecosystems has been facilitated by access to permanent sources of surface water at artificial water points (AWP), created by pastoralists to provide water for livestock (Florance et al., 2011; Letnic, Webb, Jessop, Florance, & Dempster, 2014). Most commonly, AWP consist of earthen dam reservoirs into which groundwater is pumped. Toads can readily access the water stored in earthen dams for the purposes of rehydration and reproduction (Florance et al., 2011; Letnic et al., 2014; Figure 1a,b). In some areas, AWP consist of plastic or steel storage tanks from which water is made accessible to livestock by transfer into an elevated trough (Figure 1c). In this set-up, cane toads neither have access to the water stored in tanks nor troughs. Nevertheless, a small number of toads can still be found around tanks, where they survive on the moisture seeping from small cracks or leaks at pipeline joints (Feit, Dempster, Gibb, & Letnic, 2015). However, AWP fitted with tanks do not allow cane toads to establish high-density populations, as standing water is not available for reproduction (Feit et al., 2015).

In our study area, the rangelands of the Tanami Desert in Australia's Northern Territory, pastoralists have installed open access AWP and closed access AWP. This set-up created the opportunity to conduct a large-scale natural experiment to examine direct and indirect consequences of the cane toad invasion on the structure and composition of reptile communities consisting of a large varanid lizard (the sand goanna *Varanus gouldii*; Figure 1d), small terrestrial lizards (agamids, skinks and geckos) and small arboreal lizards (geckos). We applied trophic cascade theory to evaluate how strongly interactive species can affect abundance and composition of themselves and other species at one or multiple trophic levels.

FIGURE 1 (a) Earthen dam used as reservoir at an artificial livestock watering point (AWP). (b) Dams support large numbers of cane toads (*Rhinella marina*) by allowing ready access to water for rehydration and reproduction. (c) Steel tank used as reservoir at an AWP. In comparison to dams, tanks support few toads because they allow only little access to water. (d) Sand goanna (*Varanus gouldii*)

Prior evidence indicates that cane toads suppress goanna populations (Doody et al., 2009; Feit et al., 2018). Sand goannas, in turn, can affect populations of smaller reptile species via two main pathways, predation and ecosystem engineering. The direction and magnitude of predatory effects is modulated by goannas' dietary preferences and prey ecological habits (King & Green, 1979; Olsson et al., 2005; Pianka, 1970). By leaving disused burrows that can be utilized as shelter, sand goannas provide suitable habitat for some smaller lizards via allogenic ecosystem engineering (Horner, 1991; Pianka, 2011). We therefore tested the following predictions (Figure 2): (a) sand goanna activity should be lower in the vicinity of dams due to higher lethal encounter rates between toads and goannas near dams; (b) on average, small terrestrial reptiles should be more abundant in the vicinity of dams than tanks because they are released from predation by sand goannas near dams; (c) some small terrestrial reptiles

(e.g. *Eremiascincus* spp.) could profit from sand goanna ecosystem engineering services and should be more abundant in the vicinity of tanks where goanna activity is higher; and (d) because sand goannas are predominantly terrestrial foragers, arboreal gecko species should remain unaffected by shifts in predation pressure from sand goannas.

We tested these predictions by comparing the foraging activity of sand goannas at tracking plots, the abundance and community composition of small terrestrial lizards at live trapping sites and the abundance of arboreal geckos at active search sites in habitat surrounding AWP fitted with dams and tanks respectively. In addition, we used similarity analyses (ANOSIM, SIMPER) to investigate differences in the community structure of small terrestrial lizard assemblages between live trapping sites. We recognized that in addition to the potential impacts arising from cane toads on reptiles it was also important to consider variation in habitat
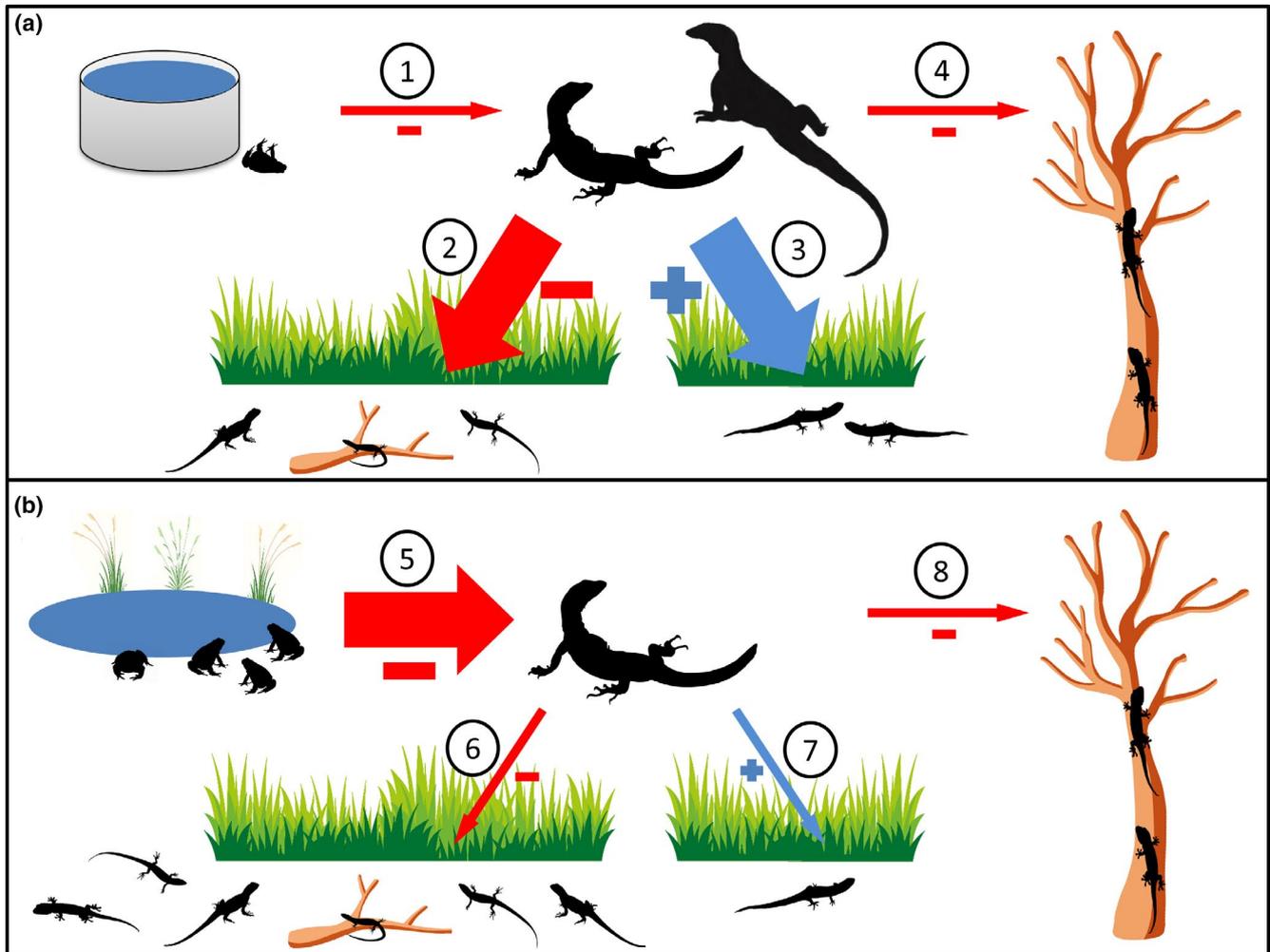
FIGURE 2 Predicted differences in negative (red) and positive (blue) population level interactions between cane toads (*Rhinella marina*), sand goannas (*Varanus gouldii*), small terrestrial lizards (agamids, skinks and geckos) and small arboreal lizards (geckos) in habitat surrounding artificial livestock watering points fitted with tanks and dams as water reservoirs. (a) Restricted access to water stored in tanks prevents cane toads from establishing dense populations; (1) negative impact of cane toads on sand goannas is low; (2) predation pressure exerted by goannas on small terrestrial lizards is high; (3) their positive impact on small terrestrial lizards through ecosystem engineering services is high; (4) their predation pressure on small arboreal lizards is low. (b) Unrestricted access to water at dams allows cane toads to establish dense populations; (5) negative impact of cane toads on sand goannas is high; (6) predation pressure exerted by goannas on small terrestrial lizards is reduced; (7) their positive impact on small terrestrial lizards through ecosystem engineering services is reduced; (8) their predation pressure on small arboreal lizards remains low

structure and other types of disturbance (i.e. grazing) that might affect abundance, community richness or species composition. Thus we tested for the effects of understorey vegetation structure and disturbances by livestock as alternate hypotheses that could influence populations of small terrestrial lizards (Feit et al., 2018; James, Landsberg, & Morton, 1999).

2 | MATERIALS AND METHODS

2.1 | Study area and time

Our study area was situated on two neighbouring livestock properties, Dungowan (16°42'S and 132°16'E; total area = 4,370 km²)

and Camfield (17°20'S and 131°17'E; 2,790 km²), in the northern margin of the Tanami Desert sand-plain in Australia's Northern Territory. The area experiences an annual mean rainfall of 580 mm, of which 96% falls in the wet season (November–April) and 4% in the dry season (May–October; Australian Bureau of Meteorology). The vegetation of the study area consists of open semi-arid savannah woodland with a sparse canopy dominated by the woody species lancewood *Acacia shirleyi*, bullwaddy *Macropteranthes kekwickii*, snappy gum *Eucalyptus leucophloia* and bloodwood *Corymbia terminalis*. The understorey is dominated by the grasses *Eriachne* spp. and *Sorghum* spp. The dominant soil type is sand.

Both properties have installed AWP with either earthen dams or tanks as reservoirs at approximately 10 km intervals.

We established study sites in habitat surrounding four AWP, two fitted with tanks and two with dams respectively. To reduce the risk of confounding environmental factors interfering with the results of our study, we selected locations with only minimal variation in underlying geology, vegetation type, land use and wild fire history. We surveyed the foraging activity of sand goannas and the abundance of cane toads and small terrestrial lizards in September 2012, April 2013, November 2013 and September 2014. Arboreal geckos were surveyed in September 2012, April 2013 and September 2014. Cane toads were first recorded in our study region during the wet season of 2007/2008 (Letnic, Webb, & Shine, 2008).

2.2 | Cane toad density at AWP

We monitored the abundance of cane toads by conducting nocturnal strip surveys along 2 m × 100 m strip transects (*n* = 4 per AWP) radiating away from the reservoir at each dam and tank respectively (Letnic et al., 2014). Visibility was enhanced by using handheld 12 V spotlights with 25 W halogen bulbs. Cane toad density was calculated as the number of individuals encountered in an area of 100 m^2.

2.3 | Goanna foraging activity

Sand goannas are difficult to survey using conventional mark-recapture techniques because they are rarely caught in traps (Letnic, Dickman, Tischler, Tamayo, & Beh, 2004). In addition, they are difficult to spot during visual surveys because of their camouflage and tendency to remain motionless when encountering potential predators. We thus estimated the relative abundance of sand goannas using previously established indices of activity that combine the occurrence of fresh tracks and foraging pits that sand goannas leave behind whilst searching for prey (Feit et al., 2018; Read & Scoleri, 2015). When walking on soft soil, sand goannas leave distinctive tail drags and claw imprints that are readily distinguishable from other animals (Read & Scoleri, 2015). When digging for prey, they leave characteristic foraging pits that exhibit deep scratch marks left by their strong forelimbs during the excavation of soil (Read & Scoleri, 2015). Both indices have been validated against known abundances in other goanna species (Anson, Dickman, Handasyde, & Jessop, 2014).

To index the level of goanna activity in the area surrounding our live trapping sites and active search sites, we established five track plots near each site. Plots were established on the access roads to each site, spaced 500 m apart and located at a maximum distance of 1 km to the respective live trapping or search site. Each track plot covered a 50 m road section that was cleared of tracks on the day prior to the survey. On each day of trapping, an observer walked along the track plots and recorded the presence or absence of recent goanna tracks. In addition, an observer walked

in a random pattern for a maximum of 2 min near each track plot, searching for recent foraging pits. To prevent double counting, observers avoided walking along the same routes twice. Track plots were scored positive for recent goanna activity when at least one of the two signs of foraging was recorded and negative when both were absent. For each 4-day survey period, an index of goanna activity was calculated as the average fraction of active plots. Activity monitoring was conducted under environmental conditions that favoured goanna activity and ensured equal and high detection probabilities across both properties (Jessop, Kearney, Moore, Lockwood, & Johnston, 2013).

2.4 | Live trapping of small terrestrial lizards

We monitored the abundances of small terrestrial lizards by live trapping on trapping grids, which were situated along unmade roads radiating from AWP. Four trapping grids, spaced 1 km apart were located within a 5 km radius from each AWP. Each trapping grid comprised four pitfall traps and four funnel traps. We used 20 L PVC buckets buried level with the ground as pitfall traps. Funnel traps (Terrestrial Ecosystems) were made of shade cloth, 750 mm long with a funnel opening of 45 mm diameter at both ends. Pitfall traps were arranged in a T-shape, spaced 10 m apart and connected with a total of 60 m drift-fence made of partially buried PVC damp course standing 20 cm. Funnel traps were located along the drift fences. Near each AWP, trapping was conducted for four consecutive days and nights during each of the four survey occasions resulting in 16 grid days with a total of 128 trap days per AWP. We emptied traps twice each day, between 7:30 a.m. and 9:00 a.m. and between 4:30 p.m. and 6:00 p.m. Captured animals were identified to species level. To avoid recaptures to enter the analysis, every individual was marked with a quick-drying permanent marker pen before release.

2.5 | Active searches for arboreal geckos

We conducted 92 nocturnal searches with a combined duration of 920 min to monitor the abundance of arboreal geckos. Active search sites were spaced 1 km apart and located within a 5 km radius from the nearest AWP. Active searches were conducted simultaneously by two observers on opposite sides of the road. Each active search session had a total duration of 10 min (5 min per observer) and was conducted between 9:00 p.m. and 11:00 p.m. Visibility was enhanced by using handheld 12 V spotlights with 25 W halogen bulbs. During active searches, observers kept a minimum distance of 50 m to the road. We searched for geckos on stems and branches of trees. A potential observers' experience bias was avoided by using random observer combinations for each survey. Sighted geckos were identified to species by their pattern and size. To prevent double counting, observers avoided walking along the same spots twice. The number of individuals sighted per

10 min of active search was used to index the abundance of arboreal geckos at each active search site.

2.6 | Cattle activity

To investigate the alternative hypothesis that habitat disturbance by grazing was influencing the abundance of small terrestrial lizards (Feit et al., 2018; James et al., 1999), we recorded the presence of cattle tracks at the same plots as established for the goanna activity surveys. An index of cattle activity for each live trapping site was expressed as the fraction of plots with fresh cattle tracks.

2.7 | Vegetation structure

We assessed the density of understorey vegetation and ground cover during all trapping sessions to create an index for habitat structure. We sampled vegetation within four randomly selected 25 m^2 subplots located in a 50 m radius surrounding each trapping grid. Within each quadrat, a checkered 20 cm × 50 cm coverboard of ten 10 cm × 10 cm squares was held 5 m away from an observer within five strata (0–20, 20–50, 50–100, 100–150 and 150–200 cm) above ground level (Colman, Gordon, Crowther, & Letnic, 2014). For analysis, we classified vegetation density into two height categories, 0–50 and 50–200 cm. Ground cover was quantified as the combined fraction of green vegetation, leaf litter and dead wood in relation to bare ground at 10 consecutive steps within the four 25 m^2 subplots.

2.8 | Statistical analysis

2.8.1 | Cane toad density, sand goanna foraging activity and abundance of small lizards

We used multivariate generalized linear modelling with generalized estimating equations (GEE; Zuur, Ieno, Walker, Saveliev, & Smith, 2009) with a normal distribution and log-link function to investigate the effects the type of AWP had on cane toad density, foraging activity of sand goannas, trapping success rates for small terrestrial lizards (captures per grid day) and detection rates for arboreal geckos (individuals sighted per 10 min active search). In addition, we used GEE to test the effects of goanna foraging activity, cattle activity, ground cover and density of understorey vegetation at 0–50 and 50–200 cm had on the trapping success rates of terrestrial skinks, agamids and geckos. Pygopods were omitted from all statistical analyses because we only caught two individuals. Because each location was subject to repeated measures, a correlation along the time axis within all measured variables was likely. To account for the nested structure, the field trip during which the survey was conducted and the identity of the AWP entered all analyses as random factors in an autoregressive correlation matrix (AR1) error structure (Zuur et al., 2009). All

multivariable generalized linear modelling was carried out using IBM SPSS Statistics 24.0.

2.9 | Community structure of small terrestrial lizards

We analysed differences in the community structure between live trapping sites near dams and tanks using a similarity analysis (ANOSIM) with 5,000 permutations and reservoir type at AWP as explanatory factor. To determine which species contributed most to the differences between live trapping sites we employed a similarity percentages (SIMPER) analysis. ANOSIM and SIMPER were performed in Primer Version 6 (Clarke & Gorley, 2006).

3 | RESULTS

3.1 | Cane toad density

The population density of cane toads was 9.4 times higher in the vicinity of AWP fitted with dams (1.31 ± 0.28 cane toads per 100 m^2) than tanks (0.14 ± 0.05, GEE, Wald χ^2 = 274.4, p < .001).

3.2 | Sand goanna foraging activity

On average, the frequency of plots with recent signs of sand goanna foraging activity in habitat surrounding AWP fitted with dams was 6.6 times lower (0.12 ± 0.03 detection probability per plot) than in habitat surrounding AWP fitted with tanks (0.79 ± 0.04; GEE, Wald χ^2 = 389.0, p < .001; Figure 3).

3.3 | Abundance of small terrestrial lizards

We caught a total of 138 small terrestrial lizards (108 at live trapping sites near dams and 30 near tanks respectively) over the course of the study. The trapping success rate of skinks, calculated as captures per grid day, was 4.2 times higher at live trapping sites in habitat surrounding AWP fitted with dams (0.55 ± 0.13 captures per grid day) than tanks (0.13 ± 0.04, GEE, Wald χ^2 = 9.58, p < .01; Table 1, Figure 3). Similarly, the trapping success rate of agamids was on average 3.4 times greater at live trapping sites in habitat surrounding AWP fitted with dams (0.17 ± 0.02) than tanks (0.05 ± 0.02, GEE, Wald χ^2 = 34.61, p < .01; Table 1, Figure 3). The trapping success rate of terrestrial geckos was 2.2 times higher at trapping sites in habitat surrounding AWP fitted with dams (0.11 ± 0.02) in comparison to tanks (0.05 ± 0.03, GEE, Wald χ^2 = 6.40, p < .05; Table 1, Figure 3). In addition, one individual each of the pygopods *Pygopus steelescotti* and *Lialis burtonis* were recorded at live trapping sites in habitat surrounding AWP fitted with dams but not recorded at tanks.

Sand goanna foraging activity had a negative effect on the trapping success rates of skinks, agamids and geckos (Table 1). Cattle
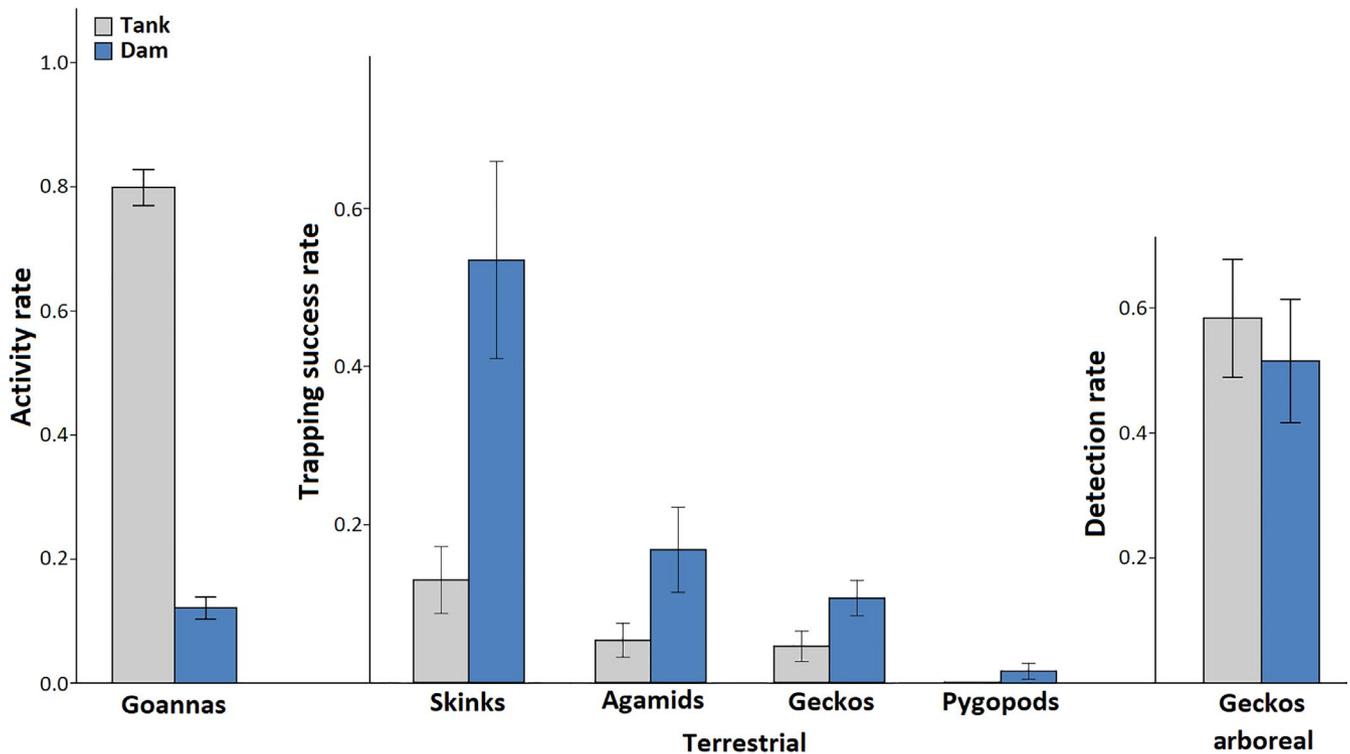
FIGURE 3 Mean foraging activity of sand goannas (*Varanus gouldii*), mean trapping success rates for terrestrial agamids, skinks, geckos and pygopods and mean detection rates for arboreal geckos in habitat within 5 km from artificial livestock watering points fitted with tanks (*n* = 2) and dams (*n* = 2) as water reservoirs. Cane toads (*Rhinella marina*) were rare at tanks and abundant at dams. Activity rates are calculated as the fraction of track plots with signs of recent goanna foraging activity along road transects. Trapping success rates are calculated as the number of individuals captured per grid day at live trapping grids consisting of four pitfall and four funnel traps. Detection rates are calculated as the number of individuals encountered during 10 min of searching at active search sites. Error bars indicate ±1 *SE*

TABLE 1 Generalized estimating equation (GEE) results for the effects of environmental variables on trapping success rates of terrestrial skinks, agamids and geckos at live trapping sites located in habitat surrounding artificial livestock watering points (AWP) fitted with tanks, where toads were rare and dams, where toads were abundant. Trapping success rates are calculated as the number of individuals captured per 100 trap days

	Skinks				Agamids				Geckos			
	PE	±1 SE	χ^2	p	PE	±1 SE	χ^2	p	PE	±1 SE	χ^2	p
AWP type dam	**0.41**	**0.10**	**16.04**	**<.01**	**0.12**	**0.02**	**34.62**	**<.001**	**0.06**	**0.03**	**6.40**	**<.05**
Goanna activity	**−0.40**	**0.15**	**6.83**	**<.01**	**−0.13**	**0.06**	**4.33**	**<.05**	**−0.05**	**0.02**	**5.04**	**<.05**
Cattle activity	0.43	0.39	1.38	.27	0.06	0.08	0.69	.41	0.12	0.12	1.08	.30
Ground cover	−0.16	0.29	0.32	.57	−0.11	0.17	0.41	.52	−0.01	0.17	0.00	.99
Veg. 50 cm	0.03	0.21	0.02	.90	−0.05	0.03	2.21	.14	**0.02**	**0.01**	**4.26**	**<.05**
Veg. 200 cm	**0.40**	**0.15**	**6.83**	**<.01**	0.05	0.03	0.03	.88	**0.02**	**0.01**	**4.39**	**<.05**

Note: Effect size of AWP type dam is relative to AWP type tank.

Abbreviations: PE, parameter estimate; *SE*, standard error; veg., density of understorey vegetation.

Bold indicates significance levels (*p* ≤ .05).

activity and ground cover had no statistical effect on either group (Table 1). Density of understorey vegetation at 0–50 cm had a positive effect on trapping success of geckos but no effect on the trapping success of skinks and agamids (Table 1). Density of understorey vegetation at 50–200 cm had a positive effect on trapping success of geckos and skinks but no effect on the trapping success of agamids (Table 1).

3.4 | Community structure of small terrestrial lizards

The ANOSIM analysis indicates significant differences in the species composition between live trapping sites located near the two reservoir types (global *R* = .205, *p* < .05). The SIMPER analysis revealed that 73.5% of the total dissimilarity of 67.2 between live trapping sites located near dams and tanks was related to

differences in trapping success rates of skinks, 15.9% related to differences in trapping success rates of agamids, 8.4% related to differences in trapping success rates of terrestrial geckos and 2.2% related to differences in trapping success rates of pygopods (Table 2).

We recorded seven additional genera at live trapping sites in habitat near dams that were not caught in traps near tanks. These taxa include two genera of skinks (*Morethia* and *Lerista*), two pygopods (*Lialis* and *Pygopus*), one agamid lizard (*Amphibolurus*) and two genera of geckos (*Lucasium* and *Rhynchoedura*; Table 2, Figure 4). At the genus level, trapping success was consistently higher near dams

than tanks with the exception of *Eremiascincus*, which was recorded 5.0 times more often in traps near tanks ($n = 5$) than dams ($n = 1$; Table 2, Figure 4).

3.5 | Abundance of arboreal geckos

The average number of arboreal geckos encountered during 10 min of active search did not differ between active search sites located in the vicinity of dams (0.52 ± 0.09) and tanks (0.58 ± 0.09; GEE, Wald $\chi^2 = 1.81$, $p = .18$; Figure 4).

TABLE 2 Results of the SIMPER analysis of trapping success rates of terrestrial skinks, pygopods, agamids and geckos comparing live trapping sites located in habitat surrounding artificial livestock watering points (AWP) fitted with tanks, where toads were rare and dams, where toads were abundant

| | | Captures | | | | | |
	Common name	Tank	Dam	D/T	Dissim.	Contr. %	Cum. %
Skinks		17	70				
Carlia amax	Two-spined rainbow-skink	2	23	↑	15.1	22.3	22.3
Ctenotus robustus	Eastern striped skink	3	12	↑	6.5	9.7	32.0
Menetia greyii	Common dwarf skink	2	10	↑	5.8	8.5	40.5
Lerista labialis	Southern sand-slider	—	7	↑	5.0	7.4	47.9
Morethia storri	Top End fire-tailed skink	—	5	↑	3.6	5.3	53.2
Lerista taeniata	Ribbon slider	—	4	↑	2.9	4.3	57.5
Menetia maini	Northern dwarf skink	1	4	↑	2.2	3.2	60.7
Carlia munda	Shaded-litter rainbow skink	2	—	↓	1.4	2.1	62.8
Eremiascincus fasciolatus	Narrow-banded sand-swimmer	3	1	↓	1.4	2.1	64.9
Eremiascincus richardsonii	Broad-banded sand-swimmer	2	—	↓	1.4	2.1	67.0
Morethia ruficauda	Lined fire-tailed skink	—	2	↑	1.4	2.1	69.1
Ctenotus helenae	Clay-soil ctenotus	1	—	↓	0.7	1.1	70.2
Ctenotus greeri	Spotted-necked ctenotus	1	—	↓	0.7	1.1	71.3
Ctenotus spaldingi	Straight-browed ctenotus	—	1	↑	0.7	1.1	72.4
Lerista orientalis	North-eastern orange-tailed slider	—	1	↑	0.7	1.1	73.5
Pygopods		—	2				
Lialis burtonis	Burton's legless lizard	—	1	↑	0.7	1.1	1.1
Pygopus steelescotti	Northern hooded scaly-foot	—	1	↑	0.7	1.1	2.2
Agamids		7	22				
Diporiphora lalliae	Lally's two-lined dragon	3	10	↑	5.0	7.4	7.4
Diporiphora magna	Yellow-sided two-lined dragon	4	11	↑	5.0	7.4	14.8
Amphibolurus gilberti	Gilbert's dragon	—	1	↑	0.7	1.1	15.9
Geckos		6	14				
Heteronotia binoei	Bynoe's gecko	5	7	↑	1.4	2.1	2.1
Lucasium stenodactylum	Sand-plain gecko	—	2	↑	1.4	2.1	4.2
Rhynchodura ornata	Western beaked gecko	—	2	↑	1.4	2.1	6.3
Diplodactylus conspicillatus	Variable fat-tailed gecko	1	3	↑	1.4	2.1	8.4
Total dissimilarity between AWP: 67.2							

Note: Captures are the combined number of individuals trapped over 32 grid days at each AWP type; D/T, arrows indicate higher (blue) or lower (orange) trapping success near dams in comparison to tanks; Dissim., average dissimilarity between captures at tanks and dams; Contr. %, contribution to the total dissimilarity; Cum. %, cumulative contribution to the total dissimilarity.
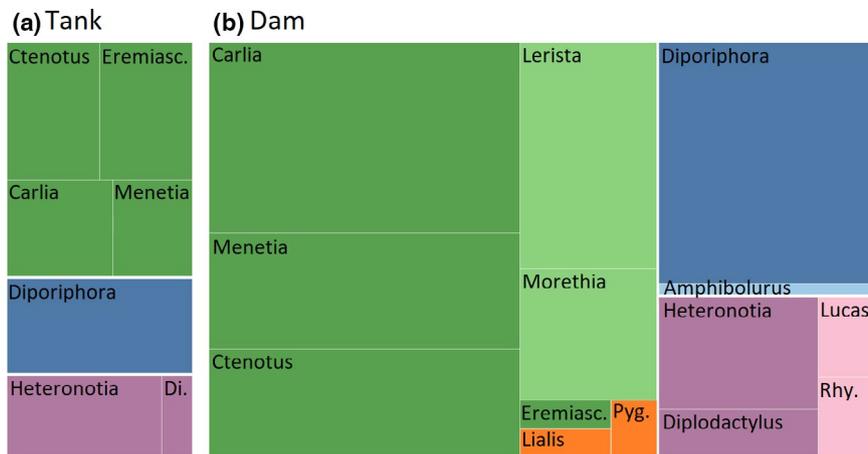
FIGURE 4 Relative trapping success for different genera of terrestrial skinks (green), agamids (blue) and geckos (purple) and pygopods (orange) at live trapping sites situated within a 5 km radius from artificial livestock watering points fitted with (a) tanks, where cane toads (*Rhinella marina*) were rare and sand goanna (*Varanus gouldii*) foraging activity was high, and (b) dams, where toads were abundant and sand goanna foraging activity was low. Box sizes are relative to the number of captures per trap day and proportional between genera and sites. Additional genera recorded at sites near dams but not recorded near tanks are highlighted with lighter coloration. Eremiasc., *Eremiascincus*; Di., *Diplodactylus*; Pyg., *Pygopus*; Lucas., *Lucasium*; Rhy., *Rhynchodura*

4 | DISCUSSION

Our results support the hypothesis that invasive cane toads can induce changes in the abundance and composition of native reptile communities through a cascade of direct and indirect population level effects. In habitat surrounding open access AWP (earthen dams), where cane toads have established high-density populations, the foraging activity of sand goannas was lower than in habitat near closed AWP (tanks), where toads occurred at very low densities. In contrast, we observed on average higher total species abundances and species richness of small terrestrial lizards in habitat near dams in comparison to tanks while skink species that are known to profit from allogenic ecosystem engineering by sand goannas were recorded more frequently near tanks. Detection rates of arboreal geckos were similar in both habitat types. These findings are in line with our a priori predictions that (a) higher encounter rates between cane toads and sand goannas have reduced the foraging activity of goannas in habitat surrounding dams in comparison to tanks, (b) the resulting decrease in predation pressure exerted by sand goannas promoted increased abundances and changes in the community structure of small terrestrial lizards near dams in comparison to tanks, (c) lizard species known to profit from goanna activity were more abundant at tanks and (d) arboreal geckos remained unaffected.

This hypothesis of a toad-induced trophic cascade is supported by previous studies documenting rapid declines of goanna populations following cane toad invasion (Doody et al., 2009; Feit & Letnic, 2015; Griffiths & McKay, 2007) and increases in the abundances of smaller terrestrial lizards following a reduction in predation pressure by goannas (Doody et al., 2013; Feit et al., 2018; Olsson et al., 2005; Read & Scoleri, 2015). In addition, the results presented in this study provide further support for the trophic cascade hypothesis by revealing diverging patterns in the community structure of

small lizards in habitat near dams and tanks that are in line with predictions based on the diet and foraging behaviour of sand goannas (Olsson et al., 2005; Read & Scoleri, 2015), and the ecology of smaller reptiles (Horner, 1991; Pianka, 2011; Read, Carter, Moseby, & Greenville, 2008).

Despite their large size—sand goannas can reach an average total length of 160 cm (Cogger, 2014)—their diet primarily consists of numerous small prey such as invertebrates, small mammals and lizards (King & Green, 1979). Small terrestrial skinks and agamids are frequently consumed by sand goannas and have been reported to comprise between 14.9% and 53.2% of ingested dietary items (King & Green, 1979; Losos & Greene, 1988). Moreover, the additional genera of skinks that were recorded at live trapping sites near dams but which remained below a threshold of detectability at live trapping sites near tanks are among the preferred prey groups of sand goannas. The pygopods recorded at live trapping sites near dams but not tanks have not been reported as dietary items of sand goannas in the literature. However, pygopods are known prey of *Varanus glebopalma*, a goanna species with a diet similar to that of sand goannas (Losos & Greene, 1988). Thus, we suggest that the differences in the abundance and community structure of small lizards at our live trapping sites resulted from predatory release that specifically favoured prey species that are most frequently preyed upon by sand goannas.

Sand goannas are primarily terrestrial predators that rarely forage on trees (Pianka, 1970; Thompson, 1995). Consequently, arboreal lizards occur infrequently in the diet of sand goannas (Losos & Greene, 1988; Pianka, 1970; Thompson, 1995). This aspect of their foraging ecology may explain why we reported an increased trapping success rates of terrestrial geckos near dams but no measureable difference in the detection rates of arboreal geckos. In addition, little overlap in the activity periods between diurnal sand goannas and nocturnal geckos further limits the potential of

sand goannas to predate on arboreal geckos which shelter within trees during the daytime. As a result, reduced goanna foraging activity in the presence of high-density cane toad populations had only negligible effects on our index of arboreal gecko abundance. Terrestrial geckos, on the other hand, are frequently preyed upon by sand goannas when they excavate burrows in which geckos shelter during the daytime (Losos & Greene, 1988; Olsson et al., 2005). Thus, we contend that predatory release stemming from the rarity of sand goannas near dams due to their poisoning by toads was the driver of the higher abundances of terrestrial geckos at dams in comparison to tanks.

The increased frequency of captures of *Eremiascincus* spp. in habitat where cane toads were rare and sand goanna activity was high is likely a result of their dependency on disused goanna burrows for shelter and/or foraging (Horner, 1991). Further support for this hypothesis comes from previous studies showing that *Eremiascincus* spp. benefit from the burrows created by other allogenic ecosystem engineers such as rabbits and bettongs (Pianka, 2011; Read et al., 2008). However, ecosystem engineering services of sand goannas extend beyond the provision of suitable habitat for small lizards. Most prominently, foraging pits left by goannas are known to act as important nutrient sinks and to promote seedling establishment (James, Eldridge, & Hill, 2009; Whitford, 1998). Thus, it is conceivable that a cane toad-induced decline in sand goanna populations could result in profound changes to nutrient cycling and vegetation recruitment in arid landscapes. We recommend that future research is conducted to further explore to what extend the cane toad invasion is affecting the structure and ecology of arid ecosystems across all trophic levels.

A shortcoming of our study is that we did not experimentally manipulate cane toad populations but instead relied upon pre-existing variations in their population densities that resulted from differences in water availability at the two types of AWP in our study area. Our study design thus only allowed for the documentation of differences in the foraging activity of sand goannas and the composition of small lizard communities between areas of already established high and low cane toad densities. Therefore, it remains a possibility that other factors, such as differences in geomorphology, vegetation, grazing pressure or fire frequency had confounding effects on the results of our study.

To minimize the effects of these potentially confounding variables, we: (a) selected our study sites in order to match soil type, land use and fire history and; (b) directly tested the alternative hypotheses that lizard communities were influenced by disturbances by livestock or the structure of understorey vegetation. As both livestock (Read, 2002) and vegetation (Jellinek, Driscoll, & Kirkpatrick, 2004) structure can have strong effects on small reptile abundance and their species richness and composition. However, cattle activity had inconclusive effects on the trapping success of skinks, agamids and geckos; whereas increases in vegetation density only had a positive effect on the trapping success rates of geckos and skinks but did not influence trapping success of agamids. Moreover, the effect of goanna activity was twice as strong and the effect of AWP type and three times as strong as the effect that vegetation cover had on the

trapping success of agamids. Thus, we are confident that variation in the interactions between cane toads, sand goannas and small lizards were the main driver of the differences in the community structure of small lizards presented in this study.

The findings of our study provide evidence that the invasion of ecosystems by non-native species can have profound effects on the structure and integrity of native communities that go beyond their often most obvious and frequently documented direct effects. Our results suggest that the invasion of cane toads triggers a trophic cascade involving toads, sand goannas and lizards. Although this cascade is unusual in that it stems from a predator dying as a consequence of attempting to eat its prey rather than the more traditional trophic cascade interaction whereby a predator consumes its prey. In the light of an increasing number of studies reporting the impacts of invasive species to transcend trophic levels in situations where they have affected keystone species (Doody et al., 2015; Feit et al., 2018; Mooney & Cleland, 2001; White et al., 2006), we contend that the paucity of evidence for such cascades might not be a reflection of their rarity but rather an indication of the necessity for further research.

DATA AVAILABILITY STATEMENT

Relevant data have been deposited in the *figshare* data repository https://doi.org/10.6084/m9.figshare.11807166.

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REFERENCES

Anderson, C. B., & Rosemond, A. D. (2007). Ecosystem engineering by invasive exotic beavers reduces in-stream diversity and enhances ecosystem function in Cape Horn, Chile. *Oecologia*, *154*(1), 141–153. https://doi.org/10.1007/s00442-007-0757-4

Anson, J. R., Dickman, C. R., Handasyde, K., & Jessop, T. S. (2014). Effects of multiple disturbance processes on arboreal vertebrates in eastern Australia: Implications for management. *Ecography*, *37*(4), 357–366. https://doi.org/10.1111/j.1600-0587.2013.00340.x

Bacher, S., Blackburn, T. M., Essl, F., Genovesi, P., Heikkilä, J., Jeschke, J. M., … Kumschick, S. (2018). Socio-economic impact classification of alien taxa (SEICAT). *Methods in Ecology and Evolution*, *9*(1), 159–168. https://doi.org/10.1111/2041-210X.12844

Cardeccia, A., Marchini, A., Occhipinti-Ambrogi, A., Galil, B., Gollasch, S., Minchin, D., … Ojaveer, H. (2016). Assessing biological invasions in European Seas: Biological traits of the most widespread non-indigenous species. *Estuarine, Coastal and Shelf Science*, *201*, 17–28. https://doi.org/10.1016/j.ecss.2016.02.014

Clarke, K. R., & Gorley, R. N. (2006). *PRIMER V6: User manual-tutorial.* Plymouth: Marine Laboratory.

Clavel, J., Julliard, R., & Devictor, V. (2011). Worldwide decline of specialist species: Toward a global functional homogenization? *Frontiers in Ecology and the Environment*, 9(4), 222–228. https://doi.org/10.1890/080216

Cogger, H. (2014). *Reptiles and amphibians of Australia.* Collingwood, Australia: CSIRO Publishing.

Colman, N. J., Gordon, C. E., Crowther, M. S., & Letnic, M. (2014). Lethal control of an apex predator has unintended cascading effects on forest mammal assemblages. *Proceedings of the Royal Society of London B: Biological Sciences*, 281(1782). https://doi.org/10.1098/rspb.2013.3094

Corbin, J. D., & D'Antonio, C. M. (2004). Competition between native perennial and exotic annual grasses: Implications for an historical invasion. *Ecology*, 85(5), 1273–1283. https://doi.org/10.1890/02-0744

Croll, D. A., Maron, J. L., Danner, E. M., & Byrd, G. V. (2003). Introduced predators transform subarctic islands from grassland to tundra. *Science*, 307, 1959–1961. https://doi.org/10.1126/science.1108485

Doody, J. S., Castellano, C. M., Rhind, D., & Green, B. (2013). Indirect facilitation of a native mesopredator by an invasive species: Are cane toads re-shaping tropical riparian communities? *Biological Invasions*, 15(3), 559–568. https://doi.org/10.1007/s10530-012-0308-8

Doody, J. S., Green, B., Rhind, D., Castellano, C., Sims, R., & Robinson, T. (2009). Population-level declines in Australian predators caused by an invasive species. *Animal Conservation*, 12(1), 46–53. https://doi.org/10.1111/j.1469-1795.2008.00219.x

Doody, J. S., Green, B., Sims, R., Rhind, D., West, P., & Steer, D. (2006). Indirect impacts of invasive cane toads (*Bufo marinus*) on nest predation in pig-nosed turtles (*Carettochelys insculpta*). *Wildlife Research*, 33(5), 349–354. https://doi.org/10.1071/WR05042

Doody, J. S., McHenry, C., Letnic, M., Everitt, C., Sawyer, G., & Clulow, S. (2018). Forecasting the spatiotemporal pattern of the cane toad invasion into north-western Australia. *Wildlife Research*, 45(8), 718–725. https://doi.org/10.1071/WR18091

Doody, J. S., Soanes, R., Castellano, C. M., Rhind, D., Green, B., McHenry, C. R., & Clulow, S. (2015). Invasive toads shift predator–prey densities in animal communities by removing top predators. *Ecology*, 96(9), 2544–2554. https://doi.org/10.1890/14-1332.1

Elton, C. C. (1958). *The ecology of invasions by animals and plants.* Chicago, IL: University of Chicago Press.

Feit, B., Dempster, T., Gibb, H., & Letnic, M. (2015). Invasive cane toads' predatory impact on dung beetles is mediated by reservoir type at artificial water points. *Ecosystems*, 18(5), 826–838. https://doi.org/10.1007/s10021-015-9865-x

Feit, B., Gordon, C. E., Webb, J. K., Jessop, T. S., Laffan, S. W., Dempster, T., & Letnic, M. (2018). Invasive cane toads might initiate cascades of direct and indirect effects in a terrestrial ecosystem. *Biological Invasions*, 20(7), 1833–1847. https://doi.org/10.1007/s10530-018-1665-8

Feit, B., & Letnic, M. (2015). Species level traits determine positive and negative population impacts of invasive cane toads on native squamates. *Biodiversity and Conservation*, 24(5), 1017–1029. https://doi.org/10.1007/s10531-014-0850-z

Florance, D., Webb, J. K., Dempster, T., Kearney, M. R., Worthing, A., & Letnic, M. (2011). Excluding access to invasion hubs can contain the spread of an invasive vertebrate. *Proceedings of the Royal Society B: Biological Sciences*, 278(1720), 2900–2908. https://doi.org/10.1098/rspb.2011.0032

Gooden, B., French, K., & Turner, P. J. (2009). Invasion and management of a woody plant, *Lantana camara* L., alters vegetation diversity within wet sclerophyll forest in southeastern Australia. *Forest Ecology and Management*, 257(3), 960–967. https://doi.org/10.1016/j.foreco.2008.10.040

Griffiths, A. D., & McKay, J. L. (2007). Cane toads reduce the abundance and site occupancy of Merten's water monitor (*Varanus mertensi*). *Wildlife Research*, 34(8), 609–615. https://doi.org/10.1071/WR07024

Horner, P. (1991). *Skinks of the northern territory.* Northern Territory Museum Handbook Series. Darwin, Australia: Northern Territory Museum of Arts and Sciences.

James, A. I., Eldridge, D. J., & Hill, B. M. (2009). Foraging animals create fertile patches in an Australian desert shrubland. *Ecography*, 32(5), 723–732. https://doi.org/10.1111/j.1600-0587.2009.05450.x

James, C. D., Landsberg, J., & Morton, S. R. (1999). Provision of watering points in the Australian arid zone: A review of effects on biota. *Journal of Arid Environments*, 41(1), 87–121. https://doi.org/10.1006/jare.1998.0467

Jellinek, S., Driscoll, D. A., & Kirkpatrick, J. B. (2004). Environmental and vegetation variables have a greater influence than habitat fragmentation in structuring lizard communities in remnant urban bushland. *Austral Ecology*, 29(3), 294–304. https://doi.org/10.1111/j.1442-9993.2004.01366.x

Jeschke, J. M., & Strayer, D. L. (2005). Invasion success of vertebrates in Europe and North America. *Proceedings of the National Academy of Sciences of the United States of America*, 102(20), 7198–7202. https://doi.org/10.1073/pnas.0501271102

Jessop, T. S., Kearney, M. R., Moore, J. L., Lockwood, T., & Johnston, M. (2013). Evaluating and predicting risk to a large reptile (*Varanus varius*) from feral cat baiting protocols. *Biological Invasions*, 15(8), 1653–1663. https://doi.org/10.1007/s10530-012-0398-3

King, D., & Green, B. (1979). Notes on diet and reproduction of the sand goanna, *Varanus gouldii rosenbergi. Copeia*, 1, 64–70. https://doi.org/10.2307/1443730

Letnic, M., Dickman, C., Tischler, M., Tamayo, B., & Beh, C.-L. (2004). The responses of small mammals and lizards to post-fire succession and rainfall in arid Australia. *Journal of Arid Environments*, 59(1), 85–114. https://doi.org/10.1016/j.jaridenv.2004.01.014

Letnic, M., Koch, F., Gordon, C., Crowther, M. S., & Dickman, C. R. (2009). Keystone effects of an alien top-predator stem extinctions of native mammals. *Proceedings of the Royal Society B: Biological Sciences*, 276(1671), 3249–3256. https://doi.org/10.1098/rspb.2009.0574

Letnic, M., Webb, J., Jessop, T. S., Florance, D., & Dempster, T. (2014). Artificial water points facilitate the spread of an invasive vertebrate in arid Australia. *Journal of Applied Ecology*, 51(3), 795–803. https://doi.org/10.1111/1365-2664.12232

Letnic, M., Webb, J. K., & Shine, R. (2008). Invasive cane toads (*Bufo marinus*) cause mass mortality of freshwater crocodiles (*Crocodylus johnstoni*) in tropical Australia. *Biological Conservation*, 141(7), 1773–1782. https://doi.org/10.1016/j.biocon.2008.04.031

Lever, C. (2001). *The cane toad: The history and ecology of a successful colonist.* Nottingham, UK: Westbury Academic & Scientific Publishing.

Losos, J. B., & Greene, H. W. (1988). Ecological and evolutionary implications of diet in monitor lizards. *Biological Journal of the Linnean Society*, 35(4), 379–407. https://doi.org/10.1111/j.1095-8312.1988.tb00477.x

Miller, K. E., & Gorchov, D. L. (2004). The invasive shrub, *Lonicera maackii*, reduces growth and fecundity of perennial forest herbs. *Oecologia*, 139(3), 359–375. https://doi.org/10.1007/s00442-004-1518-2

Mooney, H. A., & Cleland, E. E. (2001). The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences of the United States of America*, 98(10), 5446–5451. https://doi.org/10.1073/pnas.091093398

Olsson, M., Wapstra, E., Swan, G., Snaith, E., Clarke, R., & Madsen, T. (2005). Effects of long-term fox baiting on species composition and abundance in an Australian lizard community. *Austral Ecology*, 30(8), 899–905. https://doi.org/10.1111/j.1442-9993.2005.01534.x

Phillips, B., Brown, G., & Shine, R. (2003). Assessing the potential impact of cane toads on Australian snakes. *Conservation Biology*, 17(6), 1738–1747. https://doi.org/10.1111/j.1523-1739.2003.00353.x

Pianka, E. R. (1970). Notes on the biology of *Varanus gouldii flavirufus. The Western Australian Naturalist*, 11(2), 141–144.

Pianka, E. R. (2011). Notes on the ecology of some uncommon skinks in the Great Victoria Desert. *The Western Australian Naturalist*, 28, 50–60.

Pyšek, P., & Richardson, D. M. (2010). Invasive species, environmental change and management, and health. *Annual Review of Environment and Resources*, *35*(1), 25–55. https://doi.org/10.1146/annurev-environ-033009-095548

Read, J. L. (2002). Experimental trial of Australian arid zone reptiles as early warning indicators of overgrazing by cattle. *Austral Ecology*, *27*(1), 55–66. https://doi.org/10.1046/j.1442-9993.2002.01159.x

Read, J. L., Carter, J., Moseby, K. M., & Greenville, A. (2008). Ecological roles of rabbit, bettong and bilby warrens in arid Australia. *Journal of Arid Environments*, *72*(11), 2124–2130. https://doi.org/10.1016/j.jaridenv.2008.06.018

Read, J. L., & Scoleri, V. (2015). Ecological Implications of reptile meso-predator release in arid South Australia. *Journal of Herpetology*, *49*(1), 64–69. https://doi.org/10.1670/13-208

Risbey, D. A., Calver, M. C., Short, J., Bradley, J. S., & Wright, I. W. (2000). The impact of cats and foxes on the small vertebrate fauna of Heirisson Prong, Western Australia. II. A field experiment. *Wildlife Research*, *27*(3), 223–235. https://doi.org/10.1071/WR98092

Roemer, G. W., Donlan, C. J., & Courchamp, F. (2002). Golden eagles, feral pigs, and insular carnivores: How exotic species turn native predators into prey. *Proceedings of the National Academy of Sciences of the United States of America*, *99*(2), 791–796. https://doi.org/10.1073/pnas.012422499

Roy, H. E., Adriaens, T., Isaac, N. J. B., Kenis, M., Onkelinx, T., Martin, G. S., … Maes, D. (2012). Invasive alien predator causes rapid declines of native European ladybirds. *Diversity and Distributions*, *18*(7), 717–725. https://doi.org/10.1111/j.1472-4642.2012.00883.x

Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., … Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, *8*, 14435. https://doi.org/10.1038/ncomms14435

Shine, R. (2010). The ecological impact of invasive cane toads (*Bufo marinus*) in Australia. *The Quarterly Review of Biology*, *85*(3), 253–291. https://doi.org/10.1086/655116

Simon, K. S., & Townsend, C. R. (2003). Impacts of freshwater invaders at different levels of ecological organisation, with emphasis on salmonids and ecosystem consequences. *Freshwater Biology*, *48*(6), 982–994. https://doi.org/10.1046/j.1365-2427.2003.01069.x

Sousa, R., Morais, P., Dias, E., & Antunes, C. (2011). Biological invasions and ecosystem functioning: Time to merge. *Biological Invasions*, *13*(5), 1055–1058. https://doi.org/10.1007/s10530-011-9947-4

Strayer, D. L. (2010). Alien species in fresh waters: Ecological effects, interactions with other stressors, and prospects for the future. *Freshwater Biology*, *55*, 152–174. https://doi.org/10.1111/j.1365-2427.2009.02380.x

Terborgh, J., & Estes, J. A. (2010). *Trophic cascades: Predators, prey, and the changing dynamics of nature*. Washington, DC: Island Press.

Thompson, G. G. (1995). Foraging patterns and behaviours, body postures and movement speed for goannas, *Varanus gouldii* (Reptilia: Varanidae), in a semi-urban environment. *Journal of the Royal Society of Western Australia*, *78*, 107.

Van Kleunen, M., Dawson, W., Schlaepfer, D., Jeschke, J. M., & Fischer, M. (2010). Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness. *Ecology Letters*, *13*(8), 947–958. https://doi.org/10.1111/j.1461-0248.2010.01503.x

Vitousek, P. M., D'Antonio, C. M., Loope, L. L., Rejmanek, M., & Westbrooks, R. G. (1997). Introduced species: A significant component of human-caused global change. *New Zealand Journal of Ecology*, *21*(1), 1–16. Retrieved from https://www.jstor.org/stable/24054520

Walsh, J. R., Carpenter, S. R., & Vander Zanden, M. J. (2016). Invasive species triggers a massive loss of ecosystem services through a trophic cascade. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(15), 4081–4085. https://doi.org/10.1073/pnas.1600366113

White, E. M., Wilson, J. C., & Clarke, A. R. (2006). Biotic indirect effects: A neglected concept in invasion biology. *Diversity and Distributions*, *12*(4), 443–455. https://doi.org/10.1111/j.1366-9516.2006.00265.x

Whitford, W. G. (1998). Contribution of pits dug by goannas (*Varanus gouldii*) to the dynamics of banded mulga landscapes in eastern Australia. *Journal of Arid Environments*, *40*(4), 453–457. https://doi.org/10.1006/jare.1998.0464

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (Eds.). (2009). Generalised estimation equations. *Mixed effects models and extensions in ecology with R* (pp. 295–321). New York, NY: Springer.