

The impact of invasive cane toads on native wildlife in southern Australia

Christopher J. Jolly, Richard Shine & Matthew J. Greenlees

School of Biological Sciences, University of Sydney, Sydney, New South Wales 2006, Australia

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Correspondence

Christopher J. Jolly, School of Biological Sciences, University of Sydney, Sydney, NSW 2006, Australia.

Tel: 0418 259 161;

E-mail: cjol6201@uni.sydney.edu.au

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Abstract

Commonly, invaders have different impacts in different places. The spread of cane toads (*Rhinella marina*: Bufonidae) has been devastating for native fauna in tropical Australia, but the toads' impact remains unstudied in temperate-zone Australia. We surveyed habitat characteristics and fauna in campgrounds along the central eastern coast of Australia, in eight sites that have been colonized by cane toads and another eight that have not. The presence of cane toads was associated with lower faunal abundance and species richness, and a difference in species composition. Populations of three species of large lizards (land mullets *Bellatorias major*, eastern water dragons *Intellagama lesueurii*, and lace monitors *Varanus varius*) and a snake (red-bellied blacksnake *Pseudechis porphyriacus*) were lower (by 84 to 100%) in areas with toads. The scarcity of scavenging lace monitors in toad-invaded areas translated into a 52% decrease in rates of carrion removal (based on camera traps at bait stations) and an increase (by 61%) in numbers of brush turkeys (*Alectura lathami*). The invasion of cane toads through temperate-zone Australia appears to have reduced populations of at least four anurophagous predators, facilitated other taxa, and decreased rates of scavenging. Our data identify a paradox: The impacts of cane toads are at least as devastating in southern Australia as in the tropics, yet we know far more about toad invasion in the sparsely populated wilderness areas of tropical Australia than in the densely populated southeastern seaboard.

Introduction

Invasive species imperil native biodiversity (Mack et al. 2000; McGeoch et al. 2010), but invader impacts are highly heterogeneous (Melbourne et al. 2007). Some invaders have catastrophic impacts, whereas others may benefit native taxa; some native taxa are more vulnerable than others (Wonham et al. 2005; King et al. 2006; Brown et al. 2011; Simberloff 2011). Invader impact can vary even among populations of the same native species (e.g., Letnic et al. 2008; Somaweera and Shine 2012). The details of most invader impacts remain unclear because of complex direct and indirect pathways of effect (Shine 2012); a decline in one species may have positive or negative flow-on effects to many others (Doody et al. 2006; Brown et al. 2011, 2013a; Estes et al. 2011).

Impact heterogeneity necessitates studies at multiple locations throughout an invader's range (Parker et al. 1999; Melbourne et al. 2007). To assess an invader's

effects, we must measure changes in abundance of native species coincident with the presence of an invader. This task may be simple in some cases (e.g., for sessile organisms), but is more challenging if the impact falls on vagile, rare predators (Caughley 1977; Woinarski et al. 2001, 2004). To incorporate the influence of habitat and climate, studies of invader impacts on large, mobile vertebrates must employ multiple sites with a sampling design that captures a range of natural heterogeneity.

Since its introduction in 1935, the cane toad (*Rhinella marina*) has spread rapidly through Australia (Lever 2001; Kolbe, Kearney & Shine 2010). Extensive research in tropical Australia has demonstrated that the arrival of cane toads is consistently followed by population-level declines of some species of large predators that are fatally poisoned when they eat the toxic toads (Letnic et al. 2008; Doody et al. 2009). However, impacts on the (virtually unstudied) southern edge of the toads' range expansion may be very different from those in the tropics. For

example, the tropical invasion front is dominated by large adult toads; any predator that consumes a large toad will be fatally poisoned (Shine 2010). In contrast, the southern front contains small as well as large toads (McCann 2014). A small toad offers a nauseating but nonfatal meal that may allow aversion learning by predators, thereby ameliorating population-level impact (O'Donnell, Webb & Shine 2010).

The temperate-zone invasion front also facilitates spatial comparisons of affected versus unaffected sites. In the tropics, toads invade in a rapidly advancing, continuous front hundreds of kilometers wide, precluding comparisons between adjacent sites with versus without toads (Shine 2010). Thus, these studies yield before–after data on population-level impacts of toad invasion, a critical difficulty in the wet–dry tropics where even minor year-to-year variation in rainfall patterns can induce massive changes in faunal populations (Brown *et al.* 2002; Madsen *et al.* 2006; Shine and Brown 2008). Those temporal shifts make it difficult to attribute specific faunal shifts to cane toad invasion. For example, some declines in predator populations coincident with toad invasion in tropical Australia were caused by stochastic weather events, not toads (Brown *et al.* 2011).

The toad invasion into southern Australia is progressing slowly (McCann *et al.* 2014) and in a patchwork fashion (likely due to multiple translocations of toads by humans: White and Shine 2009). Adjacent areas with versus without cane toads create an opportunity for direct and concurrent comparisons. Such spatial comparisons do not overcome all of the problems associated with inferring toad impact—for example, invaded and uninvaded sites may differ in ways that affect faunal assemblages (Suarez *et al.* 1998; Bolger *et al.* 2000; Holway *et al.* 2002a,b). Nonetheless, confounding variables can be measured; and such a study is not weakened by the influence of annual variation.

Despite logistical advantages (a fragmented invasion front, a significantly higher human population, and infrastructure that facilitates research), the impact of cane toads in southern Australia has been largely ignored. We conducted surveys to quantify the characteristics of native faunal assemblages in adjacent sites that contained versus those that did not contain cane toads to test what impact toads have on fauna assemblages. We predicted that native fauna that prey on toads would be less abundant in toad-invaded areas than in areas that did not contain toads. We also surveyed habitat variables to test for potential confounding factors between invaded versus uninvaded sites, and measured rates of carrion removal to test the hypothesis that this critical ecological function would be affected by toad-induced declines of scavengers.

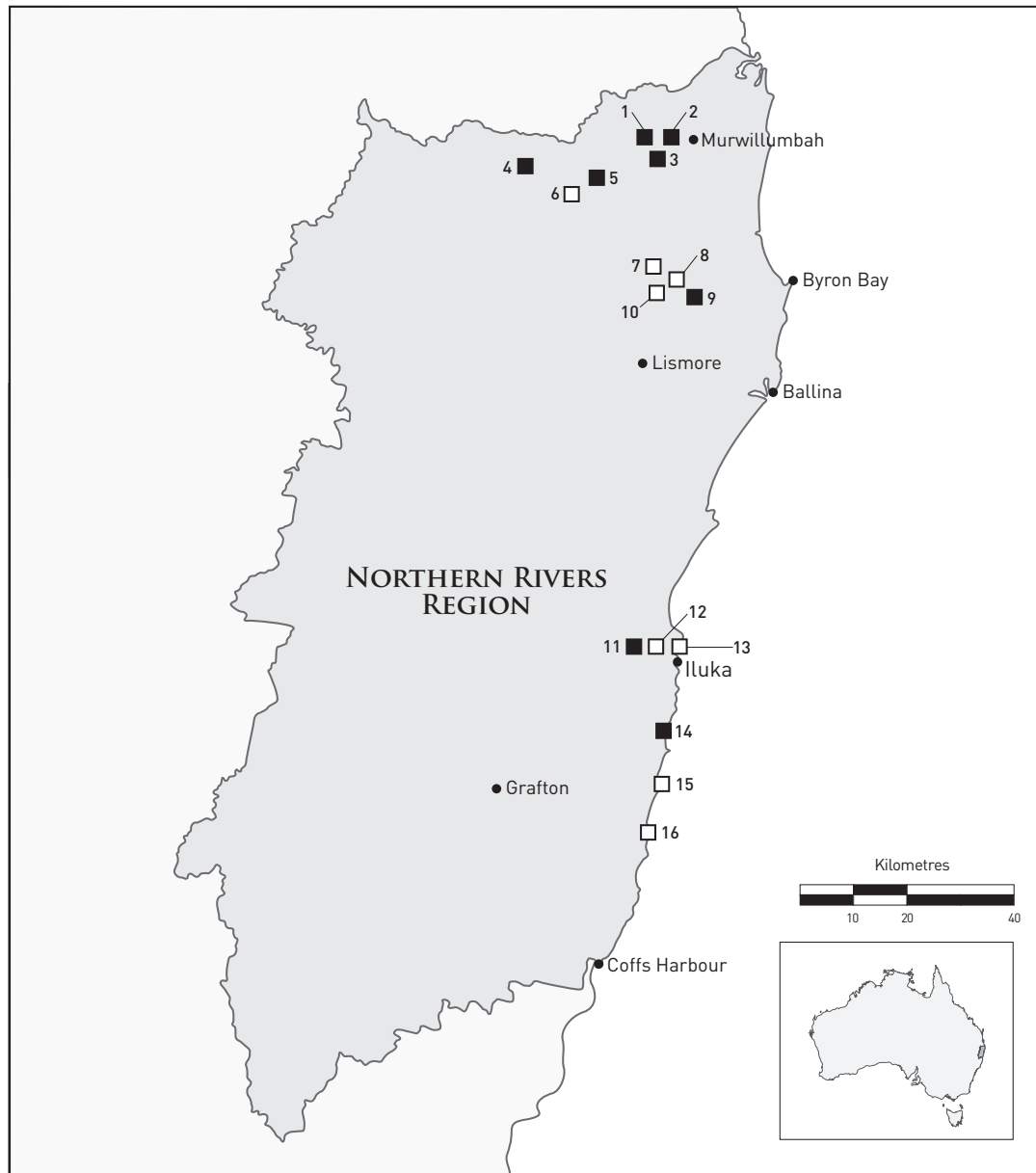
Materials and Methods

Study region

The Northern Rivers region encompasses the northeastern corner (50,266 km²) of New South Wales (NSW), Australia (DECCW 2010; Fig. 1). Although it occupies less than 10% of the state, this area supports more than 40% of the threatened species and 20% of the threatened communities of NSW (Goldingay *et al.* 1999; (DECCW 2010; Newell 2011). The region experiences a warm temperate to subtropical climate with warm humid summers (mean average maximum 26–30°C) and moderate winters (mean average minimum 6–10°C: Bureau of Meteorology 2014). Most rainfall occurs during summer and early autumn (Taylor and Goldingay 2003). Many native taxa (both ectotherms and endotherms) of this region are most active in the warmer, wetter months (September to February: Shine 1979; York *et al.* 1991; Christian and Weavers 1996; Kavanagh and Stanton 2005; Daly and Lemckert 2011), so we confined our surveys to the spring and summer months of 2013–2014.

Study species

Cane toads (*Rhinella marina*) are large (to 230-mm snout-urostyle length [SUL] and 500 g mass: Zug and Zug 1979; Brown *et al.* 2013a,b) toxic bufonid anurans (Tyler 1975; Pramuk 2006), native to Central and South America (Lever 2001). Introduced from Hawaii to northeastern QLD in 1935, this highly toxic anuran has since invaded more than 1.2 million km² of tropical and subtropical Australia (Lever 2001; Urban *et al.* 2007, 2008) and has also spread into southeastern QLD and northeastern NSW (Seabrook 1993; Lever 2003). Cane toads were introduced to NSW between 1964 and 1966, when a satellite population was established in Byron Bay (van Beurden and Grigg 1980). By 1989, this satellite population had merged to form a continuous population from the Northern Rivers region of NSW into QLD (Seabrook 1991, 1993). Presumably due to constraints of climatic conditions on toad breeding, feeding, and locomotion (Semeniuk *et al.* 2007; Kearney *et al.* 2008), cane toads are expanding their range far less rapidly in this region than at the tropical invasion front (1–3 km/year vs. 55 km/year: Seabrook 1993; Phillips *et al.* 2006, 2007; Urban *et al.* 2007). Although toads have been in NSW for almost 50 years (van Beurden and Grigg 1980), they remain patchily distributed (Seabrook 1993). That patchy distribution likely reflects anthropogenic habitat fragmentation, human-assisted dispersal, and heterogeneity of densely vegetated habitats (Seabrook 1993; Semeniuk *et al.* 2007). Hence, large tracts of suitable, but as yet



Legend

Northern Rivers Region	Toad-Exposed Campground	Toad-Free Campground	Major City/Town	
1. Korrumbyn Creek Picnic Area	2. Mt. Warning Rainforest Park	3. Clarrie Hall Picnic Area	4. Sheepstation Campground	5. Cutter's Camp Campground
6. Bar Mountain Access Picnic Area	7. Terania Creek Campground	8. Minyon Falls Picnic Area	9. Minyon Grass Picnic Area	10. Rummery Park Campground
11. Woombah Picnic Area	12. Woody Head Campground	13. Back Beach Picnic Area	14. Brooms Head Campground	15. Illaroo Campground
16. Station Creek Campground				

Figure 1. Study site locations within the Northern Rivers region, New South Wales, Australia, depicting toad-present (■) and toad-absent (□) campgrounds, which were surveyed between October 2013 and February 2014.

uncolonized, native bushland occur near long-term toad-colonized areas.

Study sites

We surveyed habitat characteristics and fauna at 16 campgrounds and picnic areas surrounded by bushland (from 28°22'S, 153°14'E to 29°57'S, 153°15'E) between October 2013 and February 2014. We selected eight sites in areas where toads are currently present (from 2 to 25 years postinvasion) and eight sites where toads are predicted to invade (Urban *et al.* 2007; Kolbe *et al.* 2010) but have not yet done so. Due to the patchy distribution of cane toads at the southern edge of their invasion, we were able to select interspersed study sites to minimize the confounding effects of latitude, longitude, elevation, climate, or vegetation. All campgrounds and picnic areas were adjacent to or within state forests or national parks (Fig. 1, see Supplementary Information for Table S1). Each site consisted of a cleared campground or picnic area plus an adjacent 5-km section of access road through native bushland.

Human-supplied food and water subsidies attract both native and invasive fauna to disturbed patches such as campgrounds, picnic areas, and landfill dumps located within reserves (Warnken *et al.* 2004; Piper and Catterall 2006; Jessop *et al.* 2012). Compared to the surrounding bushland, campgrounds and access roads also offer reduced canopy cover (and hence, greater sun exposure) at ground level, potentially facilitating reptile thermoregulation (Sartorius *et al.* 1999; Heard *et al.* 2004; McDonald 2012). Additionally, access roads provide corridors for animals to move between vegetation remnants (Taylor and Goldingay 2003), rendering the animals more easily observable during surveys. Cane toads regularly use roadways as dispersal corridors (Seabrook and Dettmann 1996; Brown *et al.* 2006) and prefer the sparse vegetation associated with human-modified areas within this region (e.g., campgrounds, golf courses, paddocks, parkland; Seabrook 1993; Semeniuk *et al.* 2007).

Fauna surveys

We examined the abundance and diversity of native predators using standardized surveys for a five-month period spanning the spring and summer peak period of faunal activity in this region. We recorded all reptile, bird (predatory and scavenger species), and mammal taxa that were encountered in these surveys (see Supporting Information for Table S2). Because populations of large elapid snakes, varanid and scincid lizards, and dasyurid marsupials have suffered severe declines as a result of the toad's tropical invasion, our surveys were designed to detect any toad-imposed differences in the abundance of these taxa.

We actively sampled each site to count reptiles, birds, and mammals. As sites differed in extent (see Supporting Information for Table S1), survey effort was standardized (1 h/survey). For the first 15 min, we actively searched for fauna in and around campground areas on foot. The remaining 45 min was conducted from a slow-moving car (20–40 km/h along 5-km road transect), from which we scanned the road for crossing animals, and roadside areas (e.g., trees, branches, fallen logs, termite mounds) for sequestered animals. Data for each campground and road transect within a site were combined to give total number of species and total number of individuals of each species for each site (standardized per 15 h of survey time). All animals observed were identified to species, using field guides and keys (taxonomy follows Pizzey and Knight 2012; Wilson and Swan 2013; Van Dyck *et al.* 2013).

During the five-month survey period, each site was sampled in 10-h-long diurnal surveys (on sunny days, >23°C), conducted at 0900–1200 h and 1300–1800 h, and in 5-h-long nocturnal surveys (on dry nights, >16°C), conducted at 1930–2330 h. To avoid bias, we rotated the time of day that each site was surveyed from day to day. For practical reasons, groups of three adjacent sites were surveyed for at least three concurrent days, in random order with respect to each group of sites and sites within each group. For statistical analysis, data for rarely encountered species (<8 individuals across all sites) were excluded.

Habitat variables

At each site, we recorded habitat variables to determine whether any spatial differences in fauna composition might be attributable to such factors rather than to the impacts of cane toads. Twenty-eight structural habitat variables (see Supporting Information for Table S3) were measured following a protocol similar to that of Brown *et al.* (2008). Beginning at the center of each campground or picnic area, we marked out two transects (north–south and east–west) into the surrounding bushland. From the origin point, we marked out four 10 × 10 m square plots centered at 20-m intervals along each transect line (within the cleared area of the site) and a further four plots at 10-m intervals in the surrounding bushland. The distances between adjacent plots were smaller in the bushland because our primary interest was the transitional zone and because of the greater apparent homogeneity of habitat conditions within the open areas. Within each plot, we estimated the proportions of the substrate covered by bare ground, lawn, leaf litter, rock, log, grass/herb, small shrub, tree trunk, and human debris (e.g., graveled roads, corrugated iron). To quantify structural aspects of the vegetation, we estimated percentage cover

of the understory, midstory, and canopy. Percentage of the ground within each plot that was exposed to direct sunlight at midday was also recorded. We noted the numbers of small (1–10 cm diameter at breast height [dbh]), medium (11–30 cm dbh), and large (>31 cm dbh) trees per plot, as well as mean tree height (Brown *et al.* 2008). In each plot, the following structural variables were also measured: leaf litter depth (cm); number of tree stumps (<5 m in height); number of fallen logs; number of hollows in tree trunks and limbs; and number of termite mounds in trees and on the ground. Additionally, we recorded the distance from the center of each plot to the closest building, tent, or car; water source; road, track, or trail; and tree.

Additional whole-campground variables measured at the commencement of surveys comprised: area cleared (m²); number of car spaces and campsites; number of campsites occupied; number of people and cars present during surveys; number of rubbish bins; number of barbecues; number of outside taps; number of access roads and walking trails; and distance (m) to nearest permanent freshwater. Landscape-scale parameters were assessed using satellite and aerial maps of the region (Google Earth). Connectivity, disturbance, and isolation were quantified by measuring cover of wooded vegetation (km²), area cleared for agricultural or residential purposes (km²), length of roadways (km), and average speed limit (km/h) of roadway, all within a 5 km radius of each site. Climatic variables were extracted from BIOCLIM climate layers to predict mean annual precipitation (mm) and mean annual maximum and minimum temperatures (°C) of each site as a function of latitude, longitude, and elevation (Busby 1991). Climatic variables were checked against long-term data sets of local weather stations (Bureau of Meteorology 2014).

Rates of carrion removal

To record rates of carrion removal in sites with and without cane toads, as well as the identity of the species responsible for carrion removal, we set up eight bait stations with remotely triggered cameras at each of 12 sites. Four bait stations were located in the bushland surrounding each campground and picnic area (in bushland vegetation plots; see above), and four bait stations were located 2 km away, along the ingress road (two on either side, and within 10 m of the road). All bait stations consisted of 10 chicken necks, lightly concealed with substrate, that were monitored by motion-sensitive infrared-triggered digital video cameras (Moultrie M-990i; EBSCO Industries, Birmingham, Alabama) for 48 h. Once this period had elapsed, we counted the remaining baits and reviewed the camera footage to determine the iden-

tity of the scavenging species. Only data from baits that were deployed during a 48-h period of suitable weather (clear, sunny days >23°C, and fine, warm nights >16°C) were used in comparisons between sites.

Statistical analysis

Habitat variables

Using the software package SPSS (SAS Institute, Cary, NC), we carried out a principal components analysis (PCA) to reduce the number of intercorrelated variables. Variances were homogeneous (Levene's test; $P > 0.05$). Bartlett's test of sphericity rejected the null hypothesis that variables were not correlated with habitats ($P < 0.05$), and identified 12 principal components (PCs; eigenvalue >1) in the rotated component matrix (using varimax with Kaiser normalization, accounting for >95% of variance in the habitat data). However, only five of these PCs were deemed to be biologically relevant. We used a multivariate analysis of variance (MANOVA) with toad exposure as the factor (two levels; cane toad present vs. absent), to explore determinants of variation in each PC axis (dependent variables). To test the roles of toads versus preexisting habitat conditions as determinants of wildlife assemblages, we constructed a series of multivariate regression models to explain (1) species richness and (2) faunal abundance at the 16 study sites. In these models, the predictor variables were toad invasion status (coded as either presence/absence or number of years since invasion [uninvaded sites were scored as 0]), the five PC habitat axis scores, and all interactions between these factors. We assessed model fit using the corrected Akaike's information criterion (AIC). We ran separate models with toad status treated as either a nominal variable (present/absent) or a continuous variable (years since toad arrival) because plausibly, the impact of toads might be immediate; or might change through time (either increasing or decreasing) if native fauna are affected through indirect processes (which might thus take significant time to eventuate), or are vulnerable only under specific environmental conditions.

Fauna surveys

Univariate analyses were conducted using general linear models in the statistical software JMP Pro 9.0 (SAS Institute). Data were visually assessed for normality, and variances were homogeneous (Levene's test, $P > 0.05$). One-factor (toad exposure) analyses of variance (ANOVA) were used to test for effects of the independent variable (two levels; cane toad present vs. absent) on total abundance and species richness of native vertebrates.

We used the program PRIMER v5 (PRIMER-E, Plymouth, UK) to assess differences in diversity and composition of native vertebrate species between sites with and without cane toads. Using the Bray–Curtis similarity coefficient (Bray and Curtis 1957), we calculated a similarity matrix with data from fauna surveys (abundance of each native vertebrate species at each site). Abundance data were fourth-root-transformed to reduce the influence of common species relative to rarer species (e.g., Clarke 1993; Quinn and Keough 2002; Lassau and Hochuli 2005). Standardization of the data was unnecessary due to prior standardization of sampling design. We employed nonmetric multidimensional scaling (nMDS: Clarke and Warwick 2001), using Bray–Curtis similarity measures, to plot a two-dimensional ordination and determine whether native vertebrate assemblages differed between sites with versus without cane toads. To compare between toad-present versus toad-absent sites in a multivariate similarity matrix, we performed analysis of similarities (ANOSIM) with 999 permutations (Sokal and Rohlf 1995; Anderson 2001; Bond and Lake 2003). As the presence of cane toads contributed to differences in species composition (see Results), we used a similarity percentage analysis (SIMPER: Clarke 1993) to identify individual species that contributed most to those differences (Clarke and Warwick 2001).

Based on those analyses, we then proceeded to compare the abundances of three species of lizard (land mullets *Bellatorias major*, eastern water dragons *Intellagama lesueurii*, lace monitors *Varanus varius*) and one species of snake (red-bellied black snake *Pseudechis porphyriacus*) between sites where toads were present versus absent. Data on the three lizard taxa were assessed independently because they were identified as having declined by SIMPER. The abundance of *P. porphyriacus* was assessed because this species has been anecdotally reported to experience severe toad-imposed population declines (Rayward 1974; Covacevich and Archer 1975; Fearn 2003; Phillips *et al.* 2003; Phillips & Fitzgerald 2004). Using JMP Pro 9.0, we compared the abundance of each species between sites where toads were present versus absent (independent variable). Because the abundance data of these individual species could not be normalized via transformation, data were analyzed using nonparametric Kruskal–Wallis analysis of variance tests (Crossland 1998; Ujvari *et al.* 2011; Crossland and Shine 2012).

Rates of carrion removal

Data conformed to the assumptions of normality and variance homogeneity. Using JMP Pro 9.0, we compared the number of chicken necks removed from bait stations (both in campgrounds and in surrounding bushland) in

both toad-present and toad-absent sites. The number of baits removed per bait station was the dependent variable, and toad exposure (two levels; toad present vs. absent) and location (two levels; campground vs. bushland) were the independent variables in a two-way analysis of variance (ANOVA). Site was included as a random factor. Differences in numbers of goanna vs. nongoanna scavengers between toad-present and toad-absent sites were compared using Fisher's exact test.

Results

Surveys of native taxa

We recorded 554 individual reptiles (of 14 species), 643 birds (of 10 species), and 250 mammals (of 10 species; see Supporting Information for Table S2). Combining counts for all native species, toad-occupied areas contained 40% fewer animals (one-way ANOVA: $F_{1,14} = 6.20$, $P = 0.03$; Fig. 2A) and 31% fewer species ($F_{1,14} = 11.82$, $P = 0.004$; Fig. 2B) than did areas without toads. The composition of faunal assemblages differed strongly between toad-present and toad-absent sites (ANOSIM: global $R = 0.36$, $P = 0.005$; 58% average dissimilarity; Fig. 3). Toad presence correlated with decreased abundances of three lizard species (lace monitors *Varanus varius*, $Z = 3.35$, $P = 0.001$; water dragons *Intellagama lesueurii*, $Z = 3.03$, $P = 0.003$; land mullets *Bellatorias major*, Kruskal–Wallis one-way ANOVA: $Z = 3.07$, $P = 0.002$; Fig. 4A–C) and increased abundance of brush turkeys (*Alectura lathami*, $Z = 2.28$, $P = 0.03$; Fig. 4E). There was no overall difference in snake abundance between toad-present and toad-absent sites (MANOVA: Wilks' Lambda = 0.013, $P = 0.67$), but one species showed a significant effect: No red-bellied black-snakes *Pseudechis porphyriacus* were encountered in sites with toads, whereas they were found in most toad-absent sites (Kruskal–Wallis one-way ANOVA: $Z = -2.14$, $P = 0.03$; Fig. 4D).

Habitat variables

From the 49 input habitat and climatic variables, we retained five PC axes (eigenvalue >4.3; each accounting for >8.9% of variance). The first axis (PC1, 19.9% of variance) loaded on campground size. PC2 (15.2% of variance) was linked to forested sites with high human resource subsidies. PC3 (11.9% of variance) was linked to leaf litter and dense vegetation. PC4 (9.2% of variance) was associated with naturally sparse vegetation, and PC5 (8.9% of variance) was associated with warm, woody sites. A MANOVA with toad presence/absence as the factor, and scores on these PC axes as dependent variables,

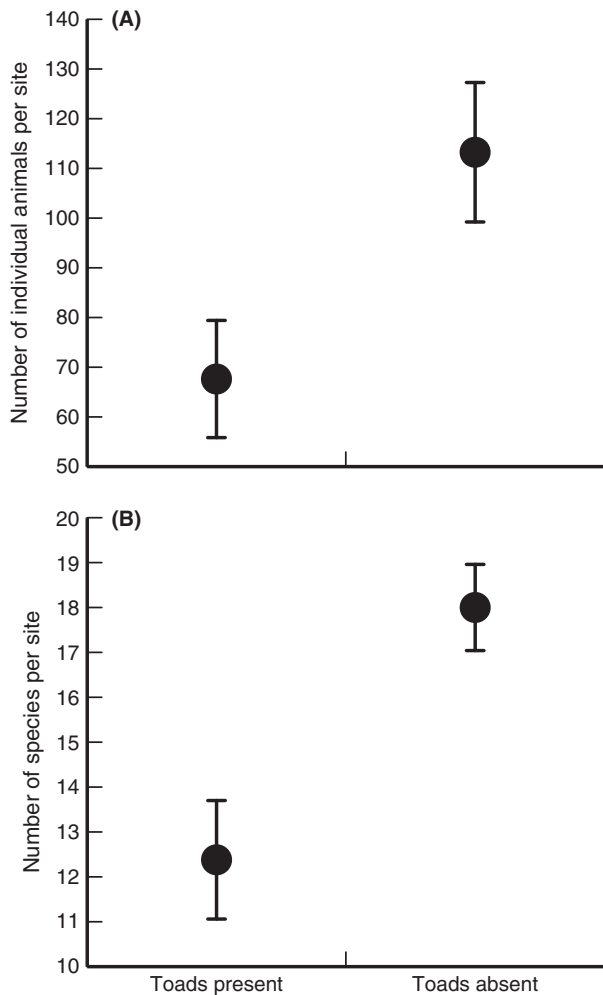


Figure 2. Impacts of cane toad presence on (A) mean abundance per site (\pm SE) and (B) mean species richness per site (\pm SE) of native fauna encountered in campgrounds and surrounding bushland areas in northeastern New South Wales, Australia.

showed no overall habitat differences between the two groups of sites (MANOVA: Wilks' Lambda = 1.63, $P > 0.05$).

Of the models we constructed to explain species richness and faunal abundance at the 16 study sites, the best-fitting models all included the impact of cane toads rather than (or as well as) habitat variation. If we included toad presence/absence as a factor, the best-fitting model for species richness included toad presence/absence and PC axis 4; the second-best (not significantly different) model included only toad presence/absence (Table 1). The results for faunal abundance were the same, except that PC1 took the role of PC4 (Table 2). If we included the impact of toads as a continuous variable (years since arrival) rather than a dichotomy, faunal species richness was best explained by a model that included only time

since toad arrival and PC3 (Table 3). For faunal abundance, the top three models were equally well supported (Δ AICc < 2), and all included time since toad arrival (one also contained PC1, one contained PC2, and one contained both PC1 and PC2; see Table 4). Thus, all of the models to explain variation among sites in faunal richness and abundance included the effect of cane toads, even after the effects of habitat variation were taken into account.

Carrion removal trials

The numbers of baits removed did not differ significantly between campground and bushland bait stations (two-way ANOVA, location: $F_{1,20} = 1.94$, $P = 0.18$; interaction location * toad exposure $F_{1,20} = 0.04$, $P = 0.84$). Despite variation among sites ($F_{20,72} = 2.20$, $P = 0.008$), fewer baits were removed from bait stations in areas where toads were present ($F_{1,20} = 24.29$, $P < 0.001$; Fig. 5). Lace monitors comprised 35 of 47 (74%) of the scavengers that removed carrion from toad-absent sites, but only 6 of 14 (43%) of the scavengers at toad-present sites (Fisher's exact test, $\chi^2 = 4.9$, $P = 0.03$).

Discussion

Invasive cane toads have massively affected the abundance and species richness of native fauna in temperate-zone Australia. In sites where toads were present, we recorded 40% fewer species and 31% fewer individuals. A causal role for toad invasion in faunal decline was supported by (1) the similarity in habitat structure and climate between toad-present versus toad-absent areas; and (2) the nature of faunal differences: The species that were less common in toad-invaded areas were reptile taxa that eat anurans. In contrast, the ground-dwelling brush turkey increased in abundance, consistent with reduced predation by goannas (Jones 1988; Goth and Vogel 2002). Our data thus suggest both direct and indirect impacts of cane toad invasion. Below, we consider native species that (1) were not affected; (2) decreased coincident with toads; and (3) increased in toad-invaded areas.

Most species were equally common in sites with and without cane toads with no negative effect on any surveyed native mammal or bird taxa. Studies on toad impact in tropical Australia have reported the same general result. Most Australian birds that prey on anurans can detect and tolerate the toad's toxin (Beckmann and Shine 2009, 2011; Beckmann et al. 2011). Although one of the bird species we counted can be killed by ingesting toads (laughing kookaburra *Dacelo novaeguineae*: Covacevich and Archer 1975; but see Ringma 2013), this vulnerability has not translated to population-level impacts. Broadly, then, direct impacts

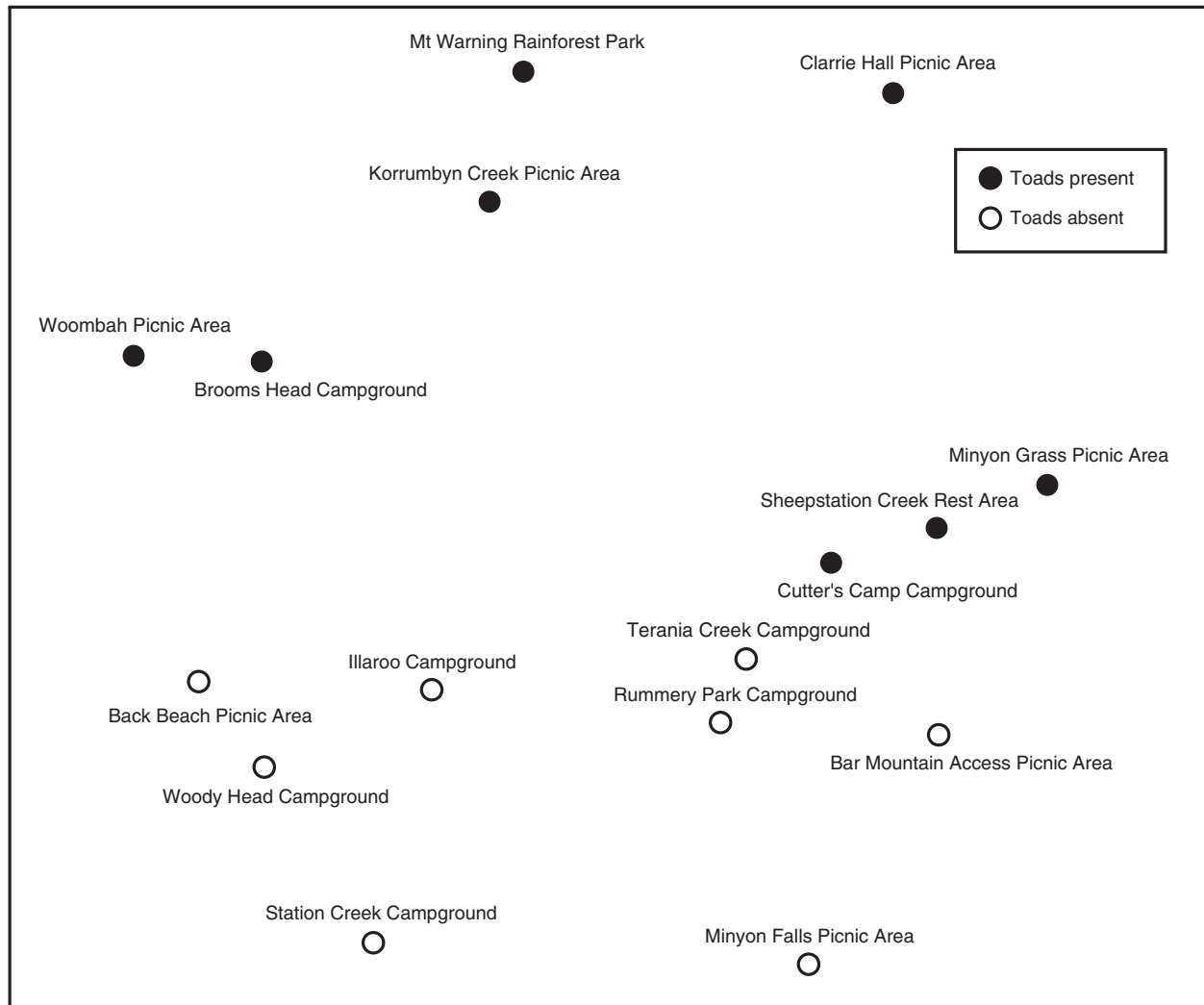


Figure 3. A nonmetric multidimensional scaling (nMDS) ordination plot showing the composition of faunal assemblages sampled from toad-present (solid circles) and toad-absent (open circles) campground sites in northeastern New South Wales, Australia (stress = 0.13).

of cane toads on predatory birds appear to be minimal, as in tropical Australia.

Similarly, we found no significant changes in mammal abundance associated with toad presence. Only three of the ten species we surveyed are likely to consume toads (fawn-footed melomys *Melomys cervinipes*; bush rat *Rattus fuscipes*; feral cat *Felis catus*). Rodents can kill and consume cane toads without ill effects (Cassels 1966; Cabrera-Guzmán et al. 2015), reflecting ancestral exposure to Asian bufonids (Fitzgerald 1990; Shine 2010). The remaining seven mammal species we surveyed (see Supporting Information for Table S2) do not eat anurans; thus, any impact to these species would have been indirect (e.g., through a reduction in goanna predation). Small sample sizes (number of individuals encountered)

weakened our ability to detect any changes, and further research would be valuable.

Our surveys failed to include some rare mammal species that might be affected by toads. In tropical Australia, the northern quoll (*Dasyurus hallucatus*) has experienced severe declines from toad invasion (Burnett 1997; O'Donnell et al. 2010; Shine 2010). Two related dasyurid species (spotted-tailed quoll *Dasyurus maculatus* and brush-tailed phascogale *Phascogale tapoatafa*) are found in northeastern (NSW) (Van Dyck et al. 2013). However, both are rare and neither was encountered during our surveys. We saw a single *P. tapoatafa* at one toad-free site, but not during standardized surveys.

Our data do not reveal any overall declines in snake abundance. Phillips et al. (2003) predicted that cane toads

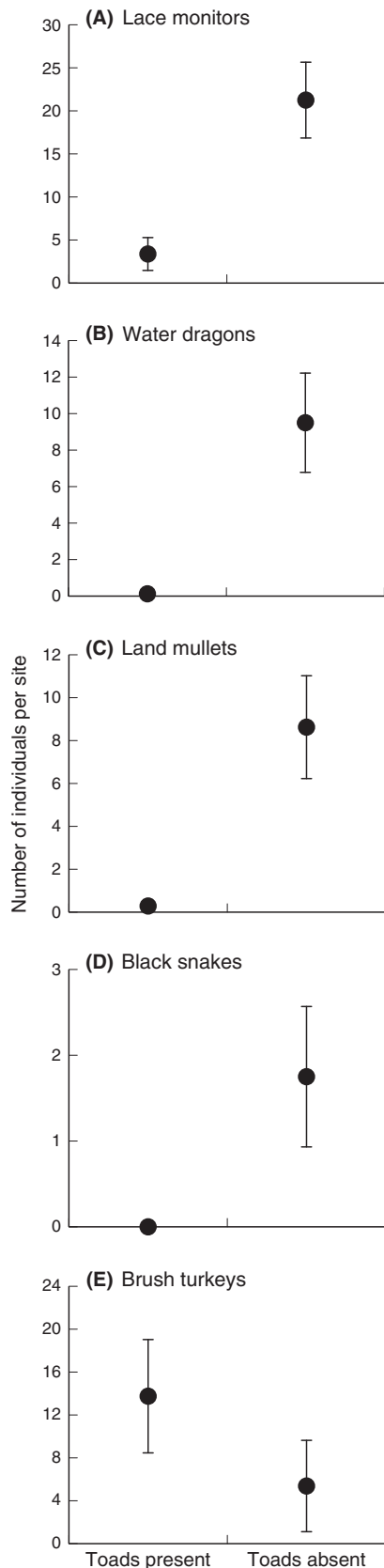


Figure 4. Impacts of cane toad presence on the mean per site abundance (\pm SE) of (A) lace monitors (*Varanus varius*), (B) water dragons (*Intellagama lesueurii*), (C) land mullets (*Bellatorias major*), (D) black snakes (*Pseudechis porphyriacus*), and (E) brush turkeys (*Alectura lathamii*) encountered during surveys of sites in northeastern New South Wales, Australia.

would cause population declines in 30% of Australia's snake species (including eight of nine species recorded in the present study), but our results suggest a more encouraging scenario. Most snake taxa, even frog specialist species (e.g., *Dendrelaphis punctulata*, *Tropidechis carinatus*) predicted to suffer toad-imposed impacts (Phillips et al. 2003), were unaffected. That lack of effect may be due to small sample sizes, to morphological or behavioral traits that render the snakes invulnerable to toads (Llewelyn et al. 2012), or to indirect positive effects (e.g., of goanna mortality) that outweigh any direct negative effects (Brown et al. 2011, 2013b; Doody et al. 2013).

Although most taxa were unaffected, toads appear to have caused catastrophic declines in populations of four reptile taxa in temperate Australia. The three lizard species affected have not been studied previously in this respect, but toad-induced declines in red-bellied blacksnakes have been reported (Pockley 1965; Rayward 1974), based on anecdotal evidence (but see Seabrook 1993). This species was absent from our toad-invaded sites. Both lace monitors and water dragons are widely sympatric with cane toads in Australia (Lever 2001; Wilson and Swan 2013), so the lack of prior reports of toad impact on these taxa is surprising.

Although these reptile species span four phylogenetically diverse families (Varanidae, Agamidae, Scincidae, and Elapidae), they share three attributes common to predators that are vulnerable to toads (Shine 2010):

- 1 Low resistance to toad toxins. Lace monitors, land mullets, and red-bellied blacksnakes can be fatally poisoned by ingesting toads (Covacevich and Archer 1975; Fearn 2003; Phillips and Shine 2006a,b; Ujvari et al. 2013). Toxin resistance is unknown for water dragons, but is low in related species (e.g., *Chlamydosaurus kingii*; Pearson et al. 2014).
- 2 Anurophagy. All of these species eat anurans (Shine 1977; Phillips and Shine 2006a,b) or are generalists with broad diets (Shea 1999; Wilson 2012). A close relative of the land mullet, the blue-tongued lizard (*Tiliqua scincoides intermedia*), has shown dramatic population declines due to toad invasion in tropical Australia (Price-Rees et al. 2010).
- 3 Large size. All four taxa are among the largest members of their respective families in Australia (Cogger 2014). Because toxin volume increases rapidly with toad

Table 1. Model selection table showing results of Akaike's information criterion tests for determinants of faunal species richness, using toad presence or absence as a dichotomous variable. The top ten highest ranked models are shown. "Prin" refers to axes of variation from principal components analysis of habitat features.

Model	Number of parameters	R^2	AIC score	Δ AICc	AIC weight
TOAD VS NO-TOAD{1-0}, Prin4	2	0.572	89.0531	0	0.2509
TOAD VS NO-TOAD{1-0}	1	0.4578	89.2014	0.1483	0.2330
TOAD VS NO-TOAD{1-0}, Prin3	2	0.4997	91.5532	2.5001	0.0719
TOAD VS NO-TOAD{1-0}, Prin3, Prin4	3	0.6149	91.7272	2.6741	0.0659
TOAD VS NO-TOAD{1-0}, Prin5	2	0.4854	92.003	2.9499	0.0574
TOAD VS NO-TOAD{1-0}, Prin4, Prin5	3	0.5981	92.4111	3.358	0.0468
TOAD VS NO-TOAD{1-0}, Prin1	2	0.4603	92.7661	3.713	0.0392
TOAD VS NO-TOAD{1-0}, Prin2	2	0.459	92.8026	3.7495	0.0385
TOAD VS NO-TOAD{1-0}, Prin1, Prin4	3	0.5784	93.1774	4.1243	0.0319
TOAD VS NO-TOAD{1-0}, Prin2, Prin4	3	0.5749	93.3087	4.2556	0.0299

Table 2. Model selection table showing results of Akaike's information criterion tests for determinants of faunal abundance, using toad presence or absence as a dichotomous variable. The top ten highest ranked models are shown. "Prin" refers to axes of variation from principal components analysis of habitat features.

Model	Number of parameters	R^2	AIC score	Δ AICc	AIC weight
TOAD VS NO-TOAD{1-0}, Prin1	2	0.5063	164.7220	0	0.2498
TOAD VS NO-TOAD{1-0}	1	0.3069	166.5150	1.7930	0.1019
TOAD VS NO-TOAD{1-0}, Prin1, Prin2	3	0.5729	166.7671	2.0451	0.0898
TOAD VS NO-TOAD{1-0}, Prin2	2	0.4370	166.8256	2.1036	0.0873
Prin2	1	0.2908	166.8832	2.1612	0.0848
TOAD VS NO-TOAD{1-0}, Prin1, Prin5	3	0.5340	168.1624	3.4404	0.0447
TOAD VS NO-TOAD{1-0}, Prin1, Prin3	3	0.5165	168.7523	4.0303	0.0333
TOAD VS NO-TOAD{1-0}, Prin1, Prin4	3	0.5085	169.0163	4.2943	0.0292
Prin2, Prin5	2	0.3504	169.1145	4.3925	0.0278
TOAD VS NO-TOAD{1-0}, Prin5	2	0.3440	169.2708	4.5488	0.0257

Table 3. Model selection table showing results of Akaike's information criterion tests for determinants of faunal species richness, using years since toad arrival as a continuous variable. The top ten highest ranked models are shown. "Prin" refers to axes of variation from principal components analysis of habitat features.

Model	Number of parameters	R^2	AIC score	Δ AICc	AIC weight
Prin3, years since toad invasion	2	0.7013	83.3006	0	0.4589
Years since toad invasion	1	0.5476	86.3062	3.0056	0.1021
Prin2, Prin3, years since toad invasion	3	0.7197	86.6440	3.3434	0.0862
Prin3, Prin5, years since toad invasion	3	0.7192	86.6752	3.3746	0.08491
Prin3, Prin4, years since toad invasion	3	0.7077	87.3178	4.0172	0.0615
Prin1, Prin3, years since toad invasion	3	0.7014	87.6589	4.3583	0.0519
Prin2, years since toad invasion	2	0.5701	89.1258	5.8252	0.0249
Prin5, years since toad invasion	2	0.5647	89.3266	6.026	0.0225
Prin4, years since toad invasion	2	0.5614	89.4456	6.145	0.0213
Prin1, years since toad invasion	2	0.5488	89.8988	6.5982	0.0169

size (Phillips and Shine 2006a,b), larger predators (which attack larger toads) are most at risk (Shine 2010).

In tropical Australia, the decline of large predatory lizards (e.g., *Varanus panoptes*) means that some native species indirectly benefit from the toad's arrival (Brown

Table 4. Model selection table showing results of Akaike's information criterion tests for determinants of faunal abundance, using years since toad arrival as a continuous variable. The top ten highest ranked models are shown. "Prin" refers to axes of variation from principal components analysis of habitat features.

Model	Number of parameters	R^2	AIC score	Δ AICc	AIC weight
Prin1, Prin2, years since toad invasion	3	0.645	163.8121	0	0.1944
Prin2, years since toad invasion	2	0.5062	164.7279	0.9158	0.1230
Prin1, years since toad invasion	2	0.4812	165.516	1.7039	0.0829
Years since invasion	1	0.3067	166.5204	2.7083	0.0502
Prin1, Prin2, Prin5, years since toad invasion	4	0.692	166.8725	3.0604	0.0421
Prin2	1	0.2908	166.8832	3.0711	0.0419
Prin2, Prin5, years since toad invasion	3	0.5571	167.3503	3.5382	0.0331
Prin1, Prin2, Prin4, years since toad invasion	4	0.6724	167.8578	4.0457	0.0257
Prin1, Prin4, years since toad invasion	3	0.5274	168.3864	4.5743	0.0197
Prin1, Prin5, years since toad invasion	3	0.5265	168.4171	4.605	0.0194

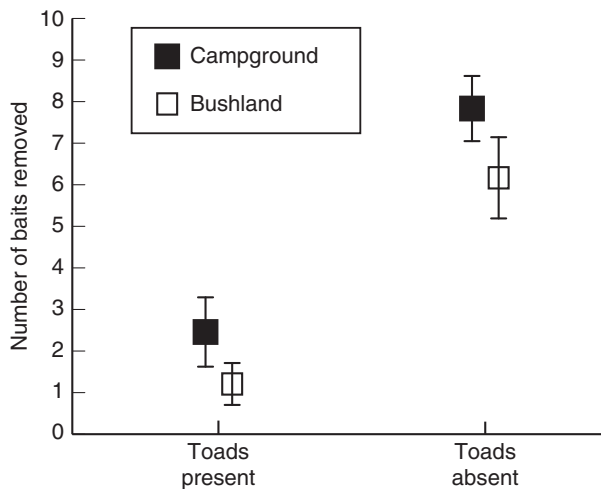


Figure 5. Impacts of cane toad presence and habitat type on mean number (\pm SE) of chicken necks removed from camera-monitored bait stations in campgrounds and surrounding bushland areas in toad-present and toad-absent areas of northeastern New South Wales, Australia.

et al. 2011, 2013a; Doody et al. 2013). Similarly, a reduction in the abundance of varanid lizards may explain the increase in the number of brush turkeys (*Alectura lathami*) in our toad-present sites. The ground-nesting habits of brush turkeys may render them (and their eggs) highly vulnerable to predation by monitors (Jones 1988; Goth and Vogel 2002). In addition to increasing brush turkey abundance, the toad-induced decline in lace monitors results in an indirect reduction to scavenging rates by 74% in toad-invaded sites. That situation also may allow increases in other scavengers (such as insects) and might create health problems for human users of the campgrounds if discarded food is left to rot. Scavengers can strongly influence the structure and function of faunal assemblages (Wilson and Wolkovich 2011).

What can be concluded, overall, about the impacts of the invasive cane toad (*Rhinella marina*) on the abundance, diversity, and composition of Australian wildlife? Although brief, our study incorporated more spatial replication and "control" sites than have been possible in the wet-dry tropics (Doody et al. 2006, 2009, 2013; Letnic et al. 2008; Phillips et al. 2010; Brown et al. 2011, 2013b; Ujvari et al. 2011). The ability to compare faunal assemblages between areas that differ mostly in exposure to toads (rather than in environmental factors) provides convincing evidence of population-level declines in native taxa due to toad arrival. Our results support the conclusion that toad impacts on native taxa are complex and proceed via both direct and indirect pathways (Shine 2010; Brown et al. 2013a). Additionally, our study provides evidence of invader impact in a region that heretofore has been largely ignored.

Cane toads are publicly vilified Australia-wide, and the public views this invasive anuran with abhorrence (Clarke et al. 2009; Shine 2010). That passion has encouraged extensive research, as well as community-based "toad busting" (Shine and Doody 2011). Given this high public profile and substantial governmental investment into cane toad issues (Shine et al. 2006), the lack of previous research on toad impacts in southern Australia is remarkable. Our study paints a bleak cautionary tale; even in an intensively studied invasive species system, major impacts on iconic native species have been overlooked. Remarkably, even anecdotal reports of cane toad impacts are rare in southern Australia, despite the dense human population. Nonchalance among the general public appears to have had flow-on effects for political and research priorities.

The scientific neglect of the toad's impacts at the southern invasion front stands in contrast to the situation in tropical Australia. Many topics related to toad biology

and ecological impacts have been investigated in remote tropical regions (review by Shine 2010). Between 1963 and 2014, 102 scientific publications assessed the ecological impacts of cane toads on the native fauna of northern Australia (i.e., north of Brisbane) compared to 14 articles on cane toad impacts in southern Australian (Shine 2010, 2014). Of those 14 articles, the most recent was completed more than 20 years ago (Seabrook 1993). This disparity in research effort is perplexing in light of the logistical difficulties that have compromised experimental designs in these tropical studies.

In summary, we found that toad invasion has caused population declines in some large anurophagous predators in temperate Australia similar to those documented in the more intensively studied tropics (Shine 2010). Ultimately, the neglect of toad impact in temperate-zone Australia reflects the fact that debates about invasive species occur within a sociopolitical framework. Geographic differences in the priority given to competing issues can influence funding incentives and research effort. The forests of northern NSW have been the focus of vigorous “environmental” battles over many years relating to forestry practices (Lemckert 1999; Kavanagh and Stanton 2005). That focus may have drawn public attention away from feral species impacts, but it is difficult to understand why scientific efforts were equally scarce. Whatever the reasons behind the disproportionate allocation of research effort toward the cane toad problem in tropical versus southern Australia, the result is clear. We have failed to recognize a major ecological problem unfolding in a place close to major cities where logistics are straightforward, and robust experimental designs are possible. If that can happen with cane toad impact, it may well happen in other ecological issues as well.

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Data accessibility

Upon acceptance of the article, data will be deposited in Dryad.

Conflict of Interest

None declared.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Study sites located in the Northern Rivers region, New South Wales, Australia.

Table S2. Vertebrate taxa recorded during surveys of campgrounds in northeastern New South Wales, Australia.

Table S3. Habitat attributes of campgrounds and bushland in toad-present versus toad-absent sites.