

# The toad less travelled: comparing life histories, ecological niches, and potential habitat of Asian black-spined toads and cane toads

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## ABSTRACT

**Context.** Invasive vertebrates have significant negative impacts on biodiversity and agricultural production worldwide. Increased connectivity among countries, through trade and tourism, is escalating the rate of introductions of vertebrate species, particularly herpetofauna, across international borders. In Australia, Asian black-spined toads (ABSTs; *Duttaphrynus melanostictus*) are one of the species most intercepted at borders. They are considered a biosecurity risk because of the potential for negative environmental impacts, similar to those caused by cane toads (*Rhinella marina*). **Aims.** We aimed to compare ABSTs with cane toads to investigate potential impacts and distribution of ABSTs in the Australian context. We also aimed to identify knowledge gaps regarding ABST biology and the potential role of cane toads in an ABST invasion in Australia. **Methods.** We undertook a literature review to obtain published data to compare the life history characteristics of ABSTs and cane toads. We also modelled climatic niche overlap and compared suitable habitat for both species in Australia. **Key results.** Our results show ABSTs and cane toads have broadly similar reproductive life histories and feeding niches. In particular, similarities include large clutch sizes, preferred oviposition sites, and diet at tadpole and adult life stages. In Australia, the species share suitable potential habitat, particularly in North Queensland, where the majority of ABST incursions have occurred. The species differ in size, call characteristics, clutch size relative to body size, and egg development rate, although the environment also influences these traits. We identify gaps in our knowledge of ABST spatial ecology, thermal tolerances, water reliance, and habitat. **Conclusions.** ABSTs pose a significant biosecurity threat to Australia. Similarities in life history to cane toads means they may have similar impacts, but may have a more limited distribution in Australia. Invasion of Australia by ABSTs would likely result in interactions with cane toads, but it is not possible to accurately determine the outcomes of those interactions without further investigation. **Implications.** Addressing knowledge gaps and quantitatively determining the potential for competition between ABSTs and cane toads will assist surveillance and response planning for ABST incursions in Australia.

**Keywords:** Asian black-spined toad, cane toad, competition, *Duttaphrynus melanostictus*, incursion, invasion, life history, niche overlap, species distribution modelling.

## Introduction

Invasive vertebrates contribute significantly to degradation of global biodiversity and have negative impacts on agricultural production and social amenity (Forsyth *et al.* 2004; Gong *et al.* 2009; Roberts *et al.* 2013; Simberloff *et al.* 2013). Greater connectivity among countries through trade and tourism has increased the rate of new species incursions globally (Lockwood *et al.* 2019; Toomes *et al.* 2020). In Australia, invasive vertebrates are a key driver of extinctions (Woinarski *et al.* 2019), are among the most prevalent threat to native threatened vertebrates (Kearney *et al.* 2019), and have economic impacts of A\$13.6B per year (Gong *et al.* 2009; Saunders *et al.* 2010; Hoffmann and Broadhurst 2016).

Various traits, including characteristics of the native range, history of establishment after introduction, diet, and habitat requirements have been used to infer the likely success of a

novel species following introduction (Toomes *et al.* 2020). Species that share similar ecological traits or niches should respond similarly to environmental conditions (Thuiller *et al.* 2005; Yu *et al.* 2017). Consequently, examining the characteristics of related or ecologically analogous species has been proposed as one method of predicting an introduced species' impact (Byers *et al.* 2002; Negussie *et al.* 2013). Although, in addition to biotic features of the invading species, successful invasion can be influenced by biotic (e.g. predators, competitors) and abiotic (e.g. resource availability) features of the new environment, propagule pressure, and human activity (e.g. alteration of environmental conditions) and their interactions (Catford *et al.* 2009).

Vertebrate incursions can occur along multiple pathways, including deliberate release, escape from the legal and illegal pet trade, and unintentional stowaways (Christy *et al.* 2007; Hulme 2015). In Australia, herpetofauna are the most frequently detected stowaways (Henderson and Bomford 2011; García-Díaz and Cassey 2014; Toomes *et al.* 2020). One species of particular concern is the Asian black-spined toad (ABST; *Duttaphrynus melanostictus*). ABSTs have been assessed as a 'Serious' establishment risk to Australia based on their habitat requirements, invasion history, and biotic traits (Bomford 2006). They are also the most commonly detected vertebrate stowaway at the Australian border, and detection rates are increasing (Tingley *et al.* 2018; Toomes *et al.* 2020).

Although ABSTs have yet not established in Australia, another Bufonid, the cane toad (*Rhinella marina*), has. Often, the potential impacts of ABSTs in Australia are considered likely to be similar to those of cane toads (Mo 2017). Cane toads provide a comparison to investigate potential impacts and spread of ABST in the Australian context and could be used as a proxy to facilitate development of surveillance and response tools for ABST incursions into Australia (Tingley *et al.* 2018; Christy 2020; Andersen *et al.* 2021). However, the life history of ABSTs is considerably less studied than that of cane toads, and there may be consequential differences between the two species. Further, the presence of cane toads in Australia could possibly influence the ability of ABST to establish and spread in Australian ecosystems through interspecific competition. Here we review the available literature to identify life history attributes of ABSTs and compare them with cane toads. We also quantify niche similarity and Australian habitat suitability for the two species, identify knowledge gaps about ABSTs, and consider the role of cane toads in a possible ABST invasion.

## Methods

### Species

Both ABSTs and cane toads have extensive native ranges (6.9 million km<sup>2</sup> and 9.7 million km<sup>2</sup> respectively), with widespread distributions on both continents and archipelagos

(van Dijk *et al.* 2004; Solís *et al.* 2009). ABSTs are a species complex of three distinct genetic lineages (Wogan *et al.* 2016), and their native distribution extends throughout south Asia (Othman *et al.* 2020). Invasive populations established in Bali in approximately 1958 and invaded many of the islands of Wallacea, West Papua in 2007 and Madagascar in approximately 2010 (Church 1960; Trainor 2009; Reilly *et al.* 2017; Vences *et al.* 2017).

The native range of cane toads has been considered to extend from southern Texas through to Brazil (Solís *et al.* 2009). Outside of their native range, they have become established more broadly than ABST, including New Guinea, Jamaica, Puerto Rico, Bermuda, Hawai'i, Taiwan, Florida, and Fiji (Easteal 1981; Lever 2001). Cane toads were introduced to Australia in 1935 as biocontrol for two major pests, the greyback beetle (*Dermolepida albohirtum*) and the Frenchi beetle (*Lepidiota frenchi*) (Mungomery and Buzacott 1936). Following establishment, cane toads increased geographic range, causing significant environmental impacts (Boland 2004; Greenlees *et al.* 2006; Letnic *et al.* 2008; Crossland *et al.* 2009; Price-Rees *et al.* 2010; Bleach *et al.* 2015). Recent genetic and morphological evaluation of cane toads has identified two species (*R. marina* and *R. horribilis*) occurring within the range historically attributed to cane toads (Acevedo *et al.* 2016). Cane toads in Australia are *R. marina* (Slade and Moritz 1998). However, because the literature relating to cane toads does not distinguish between *R. marina* and *R. horribilis* prior to 2016, and providence of populations in all invaded areas globally is not known (Sales *et al.* 2021), here we consider *R. marina* and *R. horribilis* together (*sensu* Sales *et al.* 2021).

### Literature review

The literature on the biology and ecology of ABSTs was reviewed by Christy (2020). We undertook a literature review of the biology of both cane toads and ABSTs using the online database Google Scholar to identify peer-reviewed publications and grey literature on the biology and ecology of both species. This online review was completed on 19 August 2021. In addition to online searches, we examined the reference lists of papers found in the search for additional works. For each species, we sought published data on morphology, life cycle, reproduction, habitat, diet, toxin, spatial ecology, thermal thresholds, and water requirements, and call auditory characteristics. Search terms included, but were not limited to, 'Asian black-spined toad' and 'cane toad', and their respective Latin names, followed by 'ecology', 'invasion', 'morphology', and 'physiology', etc. Where no, or limited, published data were available for ABSTs, we recorded these areas as not currently documented.

### Niche overlap

Species presence data for ABSTs and cane toads were obtained from open access databases, and ABST records

were supplemented with recent records from Madagascar (Licata *et al.* 2021; Licata and Crottini, unpubl. data). Native range and international occurrence records were collected from Global Biodiversity Information Facility (GBIF; <https://www.gbif.org>) and Australian occurrence records from Atlas of Living Australia (ALA; <https://www.ala.org.au>). We first filtered out records with an accuracy greater than 1 km<sup>2</sup>, to ensure we were using as precise a dataset as possible. We then removed multiples of records within 1-km<sup>2</sup> cells. This produced 15 001 records for cane toads and 11 311 for ABSTs. To model climatic niche (i.e. the ecological niche using only bioclimatic variables), we obtained bioclimatic variables from WorldClim (<https://www.worldclim.org>).

To produce measures of climatic niche overlap between ABSTs and cane toads, we used methods and an R script developed by Di Cola *et al.* (2017) using the *ecospat* package (Broennimann *et al.* 2021). We produced two niche overlap plots: one comparing the native climatic niches of ABSTs and cane toads, and the other comparing their total bioclimatic niches (including invaded ranges). From there, we removed highly correlated bioclimatic variables (Pearson correlation coefficient greater than 0.75), leaving us with 10 bioclimatic variables (as indicated in Supplementary Table S1).

To determine climatic overlap in the ranges of the two species, we used the occurrence records and WorldClim layers, and calculated the contribution of each bioclimatic variable as a function of the density of the records. We then used a principal component analysis (PCA) to compare the pixel values of the bioclimatic variables between the species distributions, as outlined in Broennimann *et al.* (2012) and Di Cola *et al.* (2017). These PCA scores were projected onto a grid, whereon an occurrence density grid was projected for both species, in their respective native and total ranges.

The observed niche overlap scores were calculated using Schoener's D, which varies from 0 (complete dissimilarity) to 1 (complete overlap). We created a null model for niche similarity between the two sets of compared ranges by randomising the occurrence records and calculating Schoener's D 1000 times each, then compared the observed values with the null distribution of values. If the observed value fell within this range, we concluded the ranges were no more similar than would occur by chance alone, whereas if the value fell far from the mean of the null model, the ranges were similar. Thus, a significant *P*-value ( $P < 0.05$ ) indicates there was significant similarity between the ranges of ABSTs and cane toads.

## Species distribution models

Species distribution models were constructed using maximum entropy modelling (MaxEnt V3.4). MaxEnt uses maximum entropy (i.e. most spread out, or closest to uniform), subject

to environmental features, to estimate the probability of presence of a species and generates an index of suitable habitat from 0 (lowest suitability) to 1 (highest suitability; Elith *et al.* 2011). For this, we used the same occurrence records we used for the niche modelling, as well as the filtered set of 10 bioclimatic variables that were obtained from WorldClim.

To set the threshold for discriminating suitable from unsuitable habitat, we applied the 'minimum training presence' threshold, as determined by the MaxEnt output. We used one of the lowest recommended thresholds, to avoid underestimating potential range. To determine the importance of different variables to each species, we also calculated the relative contribution of each variable and the predicted index of habitat suitability for each occurrence record (Elith *et al.* 2011).

We generated a map to compare suitable habitat for ABSTs and cane toads by calculating the difference between cane toad and ABST habitat layers. We then squared the difference to provide an absolute value of similarity. Because this was calculated after the threshold had been applied, it only calculated the overlap in relation to the extent of the species with the smaller potential range (i.e. ABSTs).

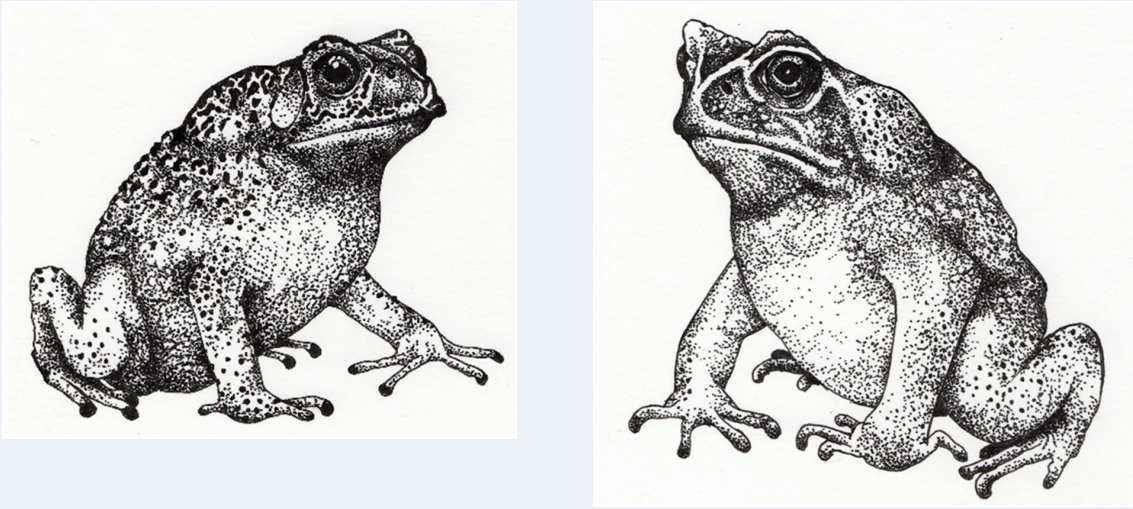
## Results

### Life history

ABSTs and cane toads share similarities in morphology, life cycle, and habitat (Table 1a–b). Both ABSTs and cane toads mature in 1–2 years and produce clutches exceeding 30 000, depending on body size (Table 1b). Adults of both species prefer open environments and disturbed areas (Table 1c). They have similar diets as both tadpoles and adults, and as generalist predators, their diets include locally available prey (Table 1d). Adult ABSTs consume mostly ants and termites, whereas cane toads eat beetles, ants, and termites, and occasionally consume several species of vertebrate (Lever 2001; Beckmann and Shine 2012). Both ABSTs and cane toads can acclimate rapidly to new environments (Table 1e).

Despite their similarities, there are notable differences between the two species, including size. Average adult ABSTs are approximately 60% the snout–vent length and 25% the body mass of the average adult cane toad (Table 1a). The reported reproductive output of ABSTs is higher than that of cane toads (40 000 cf. 30 000 eggs per clutch), with reportedly more rapid egg development (36 h cf. 72 h, respectively), (Table 1b). The reported maximum density (1800 ha<sup>-1</sup>) and rate of spread (3.3 km/year) of ABSTs are both lower than for cane toads (5000 ha<sup>-1</sup> and 60 km/year) (Table 1f). There are also differences in the call characteristics of the two species: ABST calls are longer and higher frequency than those of cane toads (Table 1g).

**Table 1.** Comparison of cane toad and ABST characteristics (references located at the bottom of the table).

Habitus	Asian black-spined toad <i>Duttaphrynus melanostictus</i>	Cane toad <i>Rhinella marina</i>
		
<b>(a) Morphology</b>		
Mean snout-vent length	Male: 72.9 mm Female: 85.3 mm	Male: 126.9 mm Female: 141.2 mm
Mean mass	Male: 46.7 g Female: 70.4 g <sup>1,2</sup>	Male: 182.0 g Female: 262.9 g <sup>6,7,8</sup>
Sexual dimorphism	Females are much larger than males. Highly variable colour pattern, usually grey to red-brown but can range from brick-red to almost black. The back is covered with warts of various sizes, which are topped with tiny dark spines. <sup>3,4</sup> Possess prominent parotoid glands. <sup>5</sup>	Females are larger than males. Males typically have yellow skin that feels like sandpaper to the touch, whereas females are smoother with dark marbled skin. Does not have the dark spines typical of ABST. <sup>9</sup> Possess prominent parotoid glands. <sup>10</sup>
<b>(b) Life cycle</b>		
Sexual reproduction	At 2 years females, males minimum 2 years. <sup>11</sup> Breed once or twice a year. <sup>11</sup>	At 1 or 2 years of age in most areas. <sup>17</sup> Breed once a year. <sup>11,18</sup>
Eggs	Prefers to lay eggs in shallow, still, or slow-flowing streams or pools of water. <sup>12</sup> Large clutches (up to 40 000 eggs per clutch, <sup>5,13</sup> in strings deposited in ponds or slow flowing streams. <sup>14</sup> Eggs take 24–36 h to develop depending on temperature. <sup>3,15</sup>	Prefers to lay eggs in shallow, still, or slow flowing water, limited vegetation. <sup>19,20</sup> Large clutches (up to 30 000 eggs per clutch) in strings deposited in ponds or slow flowing streams. <sup>6,7,21,22</sup> Eggs take 70–96 h to develop, dependent on temperature. <sup>7,17,18</sup>
Tadpoles	Tadpoles metamorphose in 25–30 days (faster when in kin groups). <sup>15</sup>	Tadpoles metamorphose in 14–28 days. <sup>21,23,24,25</sup>
Length of life	7–12 years in the wild depending on locality. <sup>3,16</sup>	10–15 years in the wild. <sup>6</sup>
<b>(c) Habitat</b>		
Tadpole	Habitat not specifically documented but adapted to survive in shallow water – tail not well developed for swimming and has weak musculature. <sup>26</sup>	Tadpoles school, usually within first 2 m of water's edge. <sup>20</sup>
Metamorph	Young toads are nocturnal and diurnal. <sup>27,28</sup> Habitat selection not documented.	Diurnal, switching to nocturnal as they grow older. <sup>32,33</sup> Metamorphs are restricted to margins of water bodies until they are old enough to disperse. <sup>22,34,35</sup>
Adult	Ground-dwelling, preference for disturbed habitat. <sup>29,30</sup> Typically detected in lowland habitats such as secondary forests, forest margins, riparian areas, and human-dominated agricultural and urban areas; uncommon in closed forest. <sup>31</sup>	Ground-dwelling, preference for open and disturbed habitat. <sup>36,37,38</sup> There is nowhere they are not found except if it is too cold. Prefer savannahs. Also common in coastal heath. <sup>39</sup>
<b>(d) Diet</b>		
Tadpole	Primary food source algae, phytoplankton and detritus. <sup>27,29,40</sup> Tadpoles can also feed on conspecific eggs and both conspecific and heterospecific adult and tadpole carrion (i.e. dead heterospecific tadpoles). <sup>41</sup>	Primarily consume algae. <sup>21</sup> Cannibalise eggs (but not tadpoles) of conspecifics. Rarely consume eggs of native anurans. <sup>21,46</sup> Intraspecific predation restricted to pre-swimming embryo stages. <sup>21</sup>

(Continued on next page)

Table 1. (Continued).

Habitus	Asian black-spined toad <i>Duttaphrynus melanostictus</i>	Cane toad <i>Rhinella marina</i>
Metamorph	Not documented	Feed largely on invertebrates such as ants, beetles, hemipterans, and arachnids. May also consume smaller conspecifics. <sup>47</sup>
Adult	Opportunistic feeder of ground-dwelling invertebrates, especially ants and termites. <sup>2,41,42,43,44</sup> Adults are generalist predators whose diets most likely dependent on what prey is available. <sup>42</sup> Only a single vertebrate has been recorded as ingested. <sup>45</sup>	Opportunistic feeder of ground-dwelling invertebrates. Diverse diet with ants, termite and beetles forming primary food sources. <sup>6,7,48,49</sup> Adults are generalist predators whose diets most likely dependent on what prey is available. <sup>6</sup> A range of vertebrates have been recorded in the diet. <sup>7,50</sup>
(e) Toxin concentration	Toxicity changes thought to be same as cane toad <sup>51</sup> but are not documented.	Concentration highest in eggs. Decreases in the tadpole and is lowest in the late tadpole–early metamorph stages, then increases after metamorphosis. <sup>52</sup>
(f) Spatial ecology		
Density	Can reach up to 1800 toads/hectare. <sup>53,54</sup>	Can reach up to 2000–5000 toads/hectare. <sup>32,59</sup>
Spatial use	Not documented	Occupy a large forage area (160 m <sup>2</sup> ) but are not site specific. <sup>6</sup> This area is smaller in the dry season, but in the wet season, toads are nomadic. <sup>8</sup>
Daily movement	Not documented	Up to 1.8 km per night, but on average 264 m per night. <sup>60,61</sup>
Rate of spread	Up to 3.3 km/year in Madagascar. <sup>55</sup>	Up to 55–60 km/year at the Australian invasion front. <sup>25,62</sup>
Thermal thresholds	Adults can tolerate exposure to 48°C for 8 days. <sup>56</sup> Tolerance at other life stages not documented. Have the capacity for rapid thermal acclimation. <sup>57</sup>	Critical thermal minimum of 10–12°C, and a critical thermal maximum of 41.5–42.5°C. <sup>6</sup> Have the capacity for rapid thermal acclimation. <sup>6,63</sup>
Water reliance	Tadpoles will metamorphose earlier in response to desiccation threat. <sup>58</sup> Adult reliance on water and desiccation tolerance not documented.	Adults can last 5 days without water <sup>64</sup> although toads in drier areas can develop cutaneous resistance to water loss. <sup>65,66</sup> Adults can tolerate up to 50% body water loss, <sup>67</sup> although behaviourally seek water after 10% body water loss. <sup>68</sup>
(g) Call profile	Average call parameters: 26 s duration, 11.69 pulses/s, 1293 Hz, although these are highly variable among populations. <sup>30</sup>	Average call parameters: 8 s duration, 15 pulses/s, 600 Hz. <sup>69,70</sup>

Data for ABST originally compiled in Christy (2020). Illustrations by CK.

References: (1) Alexander (1933); (2) Berry and Bullock (1962); (3) Bartlett *et al.* (2001); (4) Mo (2017); (5) Csurhes (2016); (6) Zug and Zug (1979); (7) Lever (2001); (8) Schwarzkopf and Alford (2002); (9) Narayan *et al.* (2008); (10) Cogger (2014); (11) Jørgensen *et al.* (1986); (12) Jayawardena *et al.* (2017); (13) Marshall *et al.* (2018); (14) Karraker and Dudgeon (2014); (15) Saidapur and Girish (2001); (16) Tyler (1989); (17) Alford *et al.* (1995); (18) Lampo and Medialdea (1996); (19) Semeniuk *et al.* (2007); (20) Lampo and de Leo (1998); (21) Hearnden (1991); (22) Shine *et al.* (2018); (23) Bayliss (1995); (24) Cabrera-Guzmán *et al.* (2011); (25) Rollins *et al.* (2015); (26) Asrafuzzaman *et al.* (2018); (27) Daniels (2005); (28) Sinha *et al.* (2001); (29) Wogan *et al.* (2016); (30) Ngo and Ngo (2013); (31) van Dijk *et al.* (2004); (32) Freeland and Kerin (1988); (33) Pizzatto *et al.* (2012); (34) Child *et al.* (2008a); (35) Brown *et al.* (2011); (36) Tingley *et al.* (2013); (37) Tingley *et al.* (2014); (38) Tingley *et al.* (2017); (39) Wijethunga *et al.* (2015); (40) Mahapatra *et al.* (2017); (41) Jamdar and Shinde (2013); (42) Norval *et al.* (2014); (43) Hui (2015); (44) Döring *et al.* (2017); (45) O'Shea *et al.* (2013); (46) Crossland (1998); (47) Pizzatto and Shine (2008); (48) Greenlees *et al.* (2006); (49) Kidera *et al.* (2008); (50) Beckmann and Shine (2012); (51) Marshall (2018); (52) Hayes *et al.* (2009); (53) McClelland *et al.* (2015); (54) Reardon *et al.* (2018); (55) Licata *et al.* (2019); (56) Deb *et al.* (1974); (57) Algiriyage *et al.* (2020); (58) Mogali *et al.* (2017); (59) Freeland (1986); (60) Phillips *et al.* (2006); (61) Phillips *et al.* (2007); (62) Urban *et al.* (2007); (63) McCann *et al.* (2014); (64) Gregg *et al.* (2019); (65) Bruschi *et al.* (2019); (66) Kosmala *et al.* (2020); (67) Krakauer (1970); (68) Jørgensen (1991); (69) Bowcock *et al.* (2008); (70) Muller *et al.* (2016).

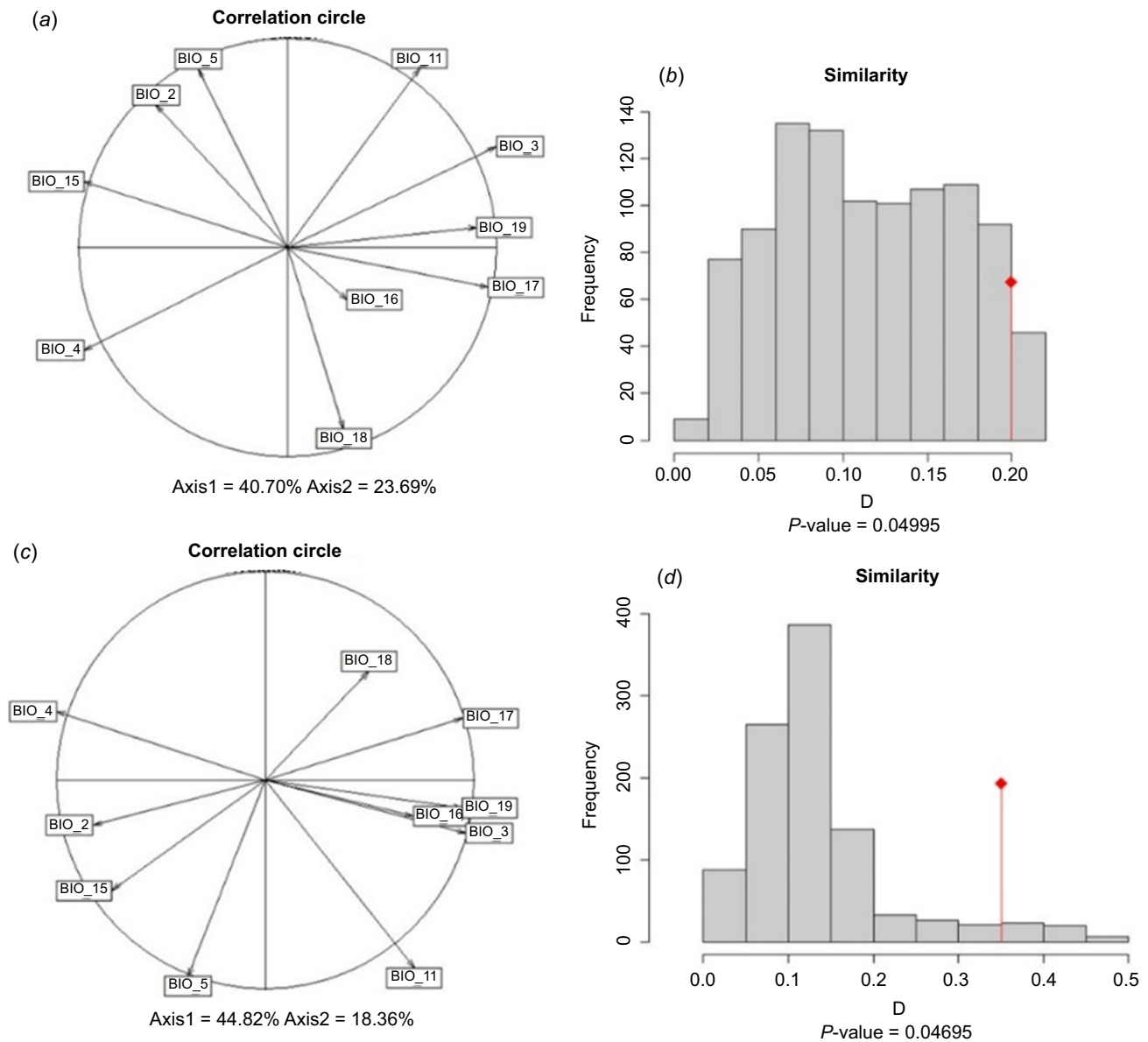
## Niche overlap

The first two principal components selected by correlation analyses explained 64.46% of the variation in the bioclimatic variables (PC<sub>1</sub> = 40.77%, PC<sub>2</sub> = 23.69%) in the native range, and in the total range explained 63.18% of the variation in the bioclimatic variables (PC<sub>1</sub> = 44.82%, PC<sub>2</sub> = 18.36%) (Fig. 1a, c, respectively). There was a large climatic niche overlap of ABSTs and cane toads in native and total ranges (Fig. 2); in the native and total ranges, almost the entire cane toad distribution is captured within the ABST distribution, suggesting a high degree of similarity both in native and introduced environments.

There were significant ( $P < 0.05$ ) climatic niche similarities in the native ( $D = 0.180$ ) and total ranges ( $D = 0.351$ ) of ABSTs and cane toads (Fig. 1; individual variable overlap Fig. S1).

## Species distribution models

The MaxEnt models had good predictive performance, producing AUC values of 0.881 for ABSTs and 0.794 for cane toads (Figs S2, S3). For ABSTs, precipitation in the wettest month (BIOL13) and the mean diurnal temperature range (BIOL2) were the two most significant factors affecting distribution, whereas low thermal variation (isothermality, BIOL3) and precipitation during the



**Fig. 1.** Comparison of climatic niches of ABSTs and cane toads in (a, b) native range only, and (c, d) total range – native and invaded. (a) and (c) represent the contribution of each climatic variable to the principal component axis for each species, and (b) and (d) represent the similarity test of the two species.

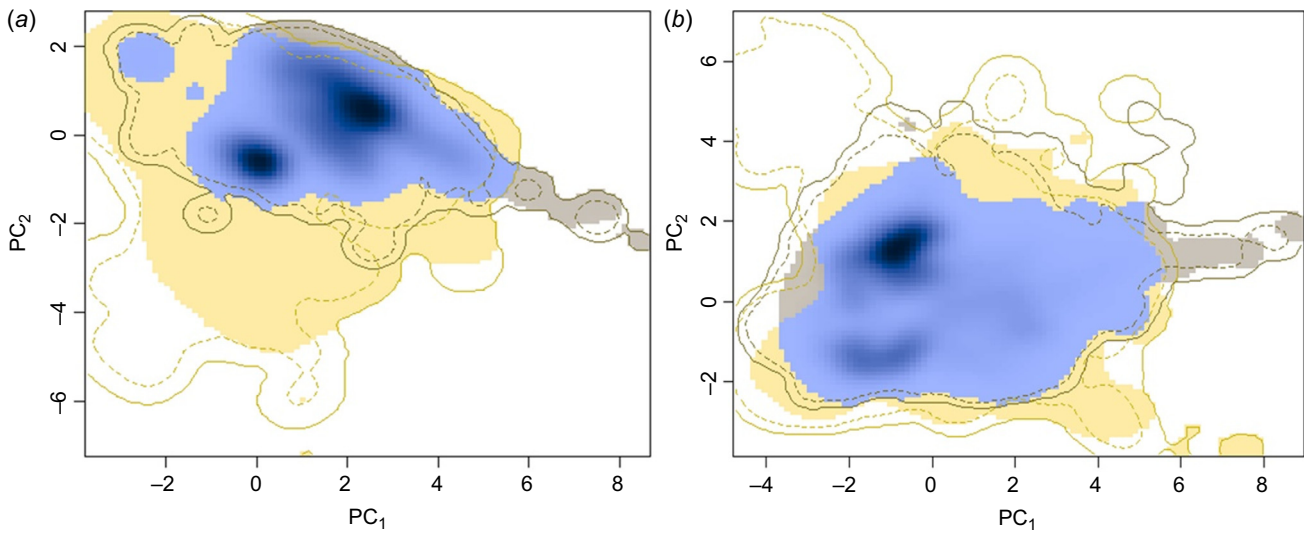
warmest quarter (BIO18) were the two most significant factors for cane toads. ABST and cane toads tolerate similar precipitation in the wettest month. However, cane toads occupy habitat with a larger mean diurnal thermal range, higher isothermality, and less precipitation in the warmest quarter compared with ABST.

Potentially suitable habitat for ABSTs in Australia covers 1.94 million km<sup>2</sup> (25.23% of the Australian landmass) compared with 7.68 million km<sup>2</sup> (99.9% of the Australian landmass) for cane toads. Areas most vulnerable to invasion by ABSTs are the northern and eastern coastlines (Fig. 3). There is considerable overlap between ABSTs and cane

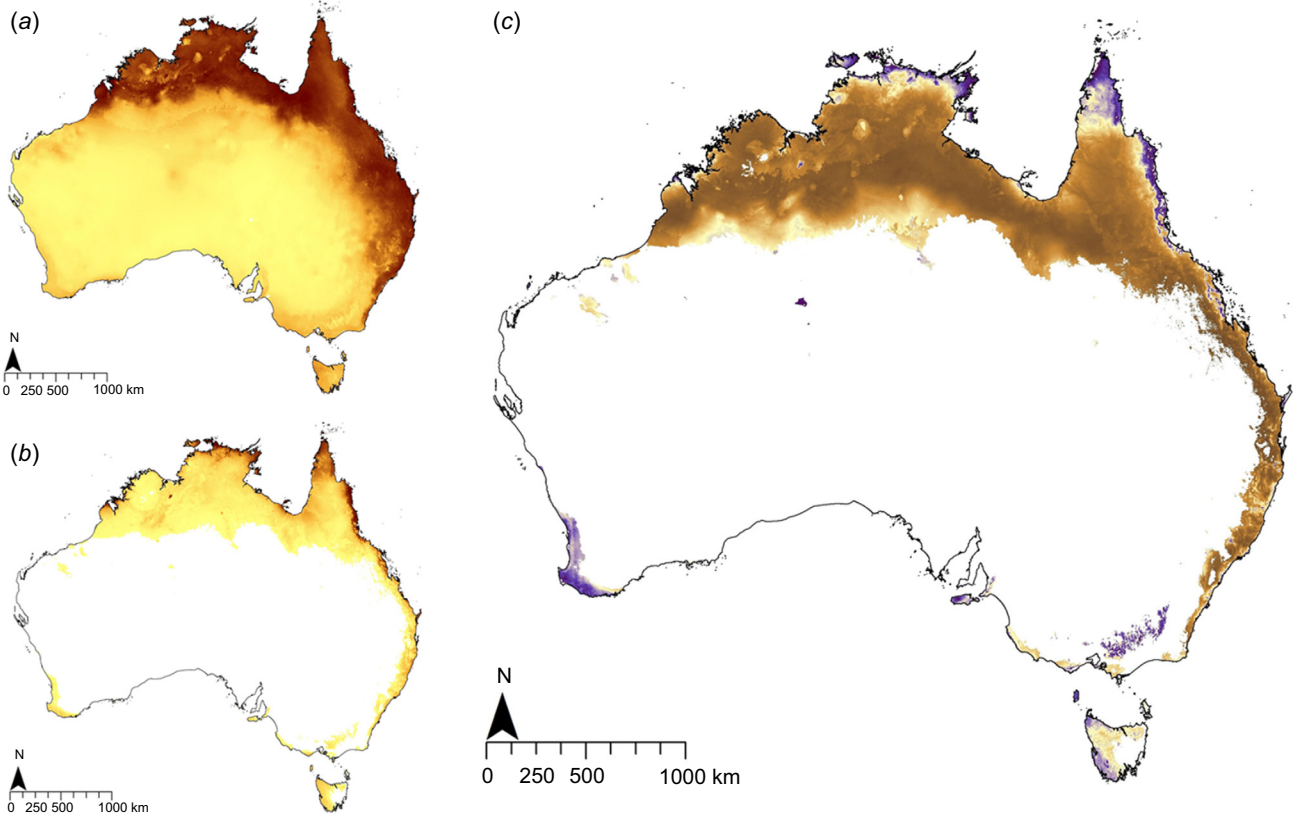
toads in potentially highly suitable habitat, especially in the northern and eastern coastal regions of the Australian mainland (dark blue areas; Fig. 3c).

## Discussion

Asian black-spined toads and cane toads share general similarities in morphology, large clutch sizes, preferred breeding sites, adult preference for disturbed land, and diet of both adults and tadpoles. In addition, they share similar climatic niches. However, there are key differences between



**Fig. 2.** Climatic niches of ABSTs (shaded yellow) and cane toads (shaded dark brown), including their overlap (blue) for (a) the native and (b) total (which included invaded) ranges. The solid line represents 100% of the available environmental space, and the dashed lines represent 50%.



**Fig. 3.** Maps of Australian MaxEnt-generated suitable habitat of (a) cane toad and (b) ABST. In these maps, the dark brown represents more suitable habitat and lighter colours represent low suitability. (c) Also presented is a map of habitat similarity between the two species. Dark purple represents habitat suitability that is highly similar (irrespective of quality) between cane toad and ABST moving to brown with increasing difference in suitability.

the species: cane toads are larger, live longer, and have been recorded reaching higher densities and spreading more rapidly than ABSTs. Asian black-spined toads reportedly produce larger clutch sizes relative to body size and have faster egg development than cane toads. However, environmental conditions, body size, and invasion stage can be highly influential in anuran reproductive output (Hudson *et al.* 2015; Kelehear and Shine 2020), development (Kearney *et al.* 2008), density (Alford *et al.* 1995; Fan *et al.* 2013; Pikacha *et al.* 2015; Licata *et al.* 2019), rate of spread (Phillips *et al.* 2010), and call characteristics (Muller 2018), so reported figures are highly context dependent. Similarities between the species suggest ABSTs could pose similar threats to Australian ecosystems as cane toads (Bomford 2006). Similarities could also contribute to priority (i.e. order of invasion) effects in locations where ABSTs attempt to establish in the presence of cane toads.

### Potential interactions between ABSTs and native species

Establishment of ABSTs in Australia would create novel interactions in Australian ecosystems. The impacts of ABSTs on ecosystems in their invaded range are poorly documented, although they competitively displace native Indonesian toads (*Ingerophrynus biporcatus*) (Church 1960; Iskander 2004). Given the similarities in life histories, ABSTs, like cane toads, may have both top-down and bottom-up trophic effects (Shine 2010) and compete with native species. For example, adult cane toads in Australia consume vast quantities of invertebrates, and in doing so can out-compete native anurans (Greenlees *et al.* 2006). Tadpoles of cane toads and native Australian frog species can also compete, reducing the number of native metamorphs (Crossland *et al.* 2009). Further, cane toads compete with native frogs for acoustic space (Hu *et al.* 2009; Brodie *et al.* 2021), leaving fewer gaps of silence for native frogs to exploit (Bleach *et al.* 2015). The dominant call frequency of ABSTs overlaps those of several native frogs in Australia (at least 28 species compared with approximately 12 species overlapping with cane toads (Allen-Ankins, pers. comm.; Allen-Ankins and Schwarzkopf 2022)), and their establishment in Australia could potentially reduce calling behaviour of native frogs (Taylor *et al.* 2017).

In terms of bottom-up effects, cane toads pose risks to some native species that prey on them, primarily because Australian predators have little resistance to bufotoxins (Phillips *et al.* 2003; Boland 2004; Shine 2010). Mortality from consumption of toads can significantly reduce predator populations at the invasion front, where species are naïve to cane toads (Letnic *et al.* 2008; Doody *et al.* 2009, 2015; Jolly *et al.* 2016). The similarities in life history combined with the difference in size between ABSTs and cane toads mean it is likely that ABSTs would have similar effects on native species to those of cane toads. The difference in adult size between the

two species warrants investigation of the potential impacts on native predators of having a second, smaller toxic toad in Australia.

### Potential interactions between ABST and cane toads

Given the species are related, share similarities in life history and climatic niches with potential habitat overlap, ABST establishment in Australia would mean they would likely interact with cane toads. When a species invades an ecosystem, it can be met with biotic resistance from resident species (Von Holle and Simberloff 2005). In some cases where an invasive species has already established, priority effects can impact the invasion success of later arriving species (Shulman *et al.* 1983; Wainwright *et al.* 2012). Priority effects can be more pronounced for closely related species (Tan *et al.* 2012). Cane toads are established across much of the potential ABST habitat in northern Australia. Although not universal, greater body size can provide a competitive advantage over similar species (Martin and Ghalambor 2014), and has been identified as an important factor in successful amphibian introductions (Tingley *et al.* 2010). Both priority effects and larger body size may convey a competitive advantage to cane toads. Moreover, Vidal-García and Keogh (2017) have proposed that the success of cane toads in Australia is due to their distinct morphology, coupled with a broad trophic niche breadth, allowing them to exploit an empty niche among Australian anurans. The morphological and dietary similarities between ABSTs and cane toads indicate scope for interspecific competition.

Interspecific competition between cane toads and ABST could result in constriction, divergence, or, conversely, expansion of the ABST or cane toad ecological niche (Dominguez Almela *et al.* 2021). An extreme, but unlikely, outcome could be competitive exclusion (Bøhn *et al.* 2008; Simha *et al.* 2022). Change of the ecological niche of ABSTs caused by interspecific competition could have flow-on effects for Australian ecosystems. Examination of a location where the two species co-occur as invasive species would be instructive. However, although the global introduced ranges of ABSTs and cane toads overlap in New Guinea (van Winkel and Lane 2012; Licata *et al.* 2019), they do not occur in sympatry there (Richards, pers. comm.; Menzies, pers. comm.). As such, it is not possible to determine the extent of interspecific competition between the species or any combined impacts of both species on native ecosystems using *in situ* observations.

An approach that may help estimate comparative impacts of the two species is to compare their functional and numerical responses. Comparative functional response (CFR) aims to quantify the resource consumption efficiency of functionally analogous species (Dick *et al.* 2014). Functional responses are assessed as a combination of the species attack rate and prey-handling time (Dick *et al.* 2013). CFR has been conducted between potentially invasive species and analogous native



species to predict the impact of the invasive species (Dick *et al.* 2014; Laverty *et al.* 2017; Dickey *et al.* 2020). By combining functional responses with proxies for numerical responses, relative impact potential (RIP) further quantifies potential ecological impacts of invasive species and can be used to examine the potential role of competition in invasions (Dickey *et al.* 2020). Using an RIP approach to compare possible impacts of ABST and cane toads may shed light on potential competition; however, this analysis focuses entirely on competition for food. Cane toads and ABSTs may compete for other resources (e.g. breeding sites, acoustic space) as well.

A key difference in the invasion history of cane toads and ABST in Australia is propagule pressure. Thousands of captive-bred cane toad tadpoles were deliberately liberated in 1935 (Froggatt 1936; Lever 2001), and approximately 112 ABST (102 alive) have been intercepted in Australia since 1999 (Tingley *et al.* 2018). Although the difference in propagule pressure is marked, introductions of relatively small numbers of ABST may still pose a significant establishment threat due to the high reproductive capacity of ABST. In Madagascar, the ABST population was likely established from accidental introduction of a limited number of individuals released into highly suitable habitat surrounding ports (McClelland *et al.* 2015; Pearson 2015). This population spread over 10 800 ha and reached over 4 000 000 post-metamorphic toads in the 4–8 years following incursion (Reardon *et al.* 2018). This emphasises how rapidly a species can proliferate when the novel environment is highly suitable, even with relatively small founding populations.

### Species distribution modelling

Our species distribution modelling shows marked differences in the area of suitable habitat for the two species in Australia. Our cane toad species distribution model for Australia is broadly similar to recent modelling (Kearney *et al.* 2008; Andersen *et al.* 2021; Sales *et al.* 2021) and indicates that much of northern and eastern Australia includes highly suitable habitat for the species. In comparison, our species distribution model for ABST suggests that suitable habitat is largely constrained to a narrow band of eastern northern Australia. This overlaps with the locations where border interceptions of ABST at ports have been most frequent (Tingley *et al.* 2018). Our modelling is consistent with models by Andersen *et al.* (2021) and Page *et al.* (2008), although these authors suggest a broader range of suitable habitat across northern Australia, with highest habitat suitability away from the coast. Our ABST species distribution modelling differs from that of Tingley *et al.* (2018), who suggest a more south-easterly potential distribution of ABST. Differences are likely due to different variable selection used in the analyses.

There is a notable difference between the climatic niche overlap, where cane toad climatic niche falls within that of ABSTs, and the spatial distribution modelling, where the

potential Australian distribution of ABSTs falls within that of cane toads. There is significant overlap between the two species in terms of precipitation of the wettest month, although ABST occupy habitat that has comparatively more precipitation during the summer and areas with less precipitation in the dry season. It is possible that ABST habitat in Australia is more limited because cane toads can occupy habitat with a wider diurnal thermal range, higher isothermality, and lower precipitation in the warmest quarter of the year than ABST (Fig. S1). These differences may also occur because we lack ABST records within Australia (unlike cane toads), influencing the accuracy of distribution mapping and cropping the global habitat suitability to Australia.

According to our species distribution modelling, the area of potential habitat for ABST in Australia is almost entirely contained within the area of suitable habitat for cane toads. The overlap of highly suitable habitat occurs predominantly in coastal north-east Queensland, the north-east of the Northern Territory, and the western Kimberley. It is important to note, however, that cane toads have exhibited shifts in their realised climatic niche during their invasion of Australia, expanding their range well beyond that predicted from the native range (Tingley *et al.* 2014; Sales *et al.* 2021). When climatic niche shifts were examined for ABSTs alone, there was a significant similarity between their native and introduced ranges. A lack of an observed shift in their climatic niche may be due to their presently limited international distribution and, therefore, little opportunity to spread beyond their current climatic envelope. As such, ABST could potentially adapt to new climatic niches.

### Knowledge gaps

ABSTs are not well studied across their range. In comparison, cane toads have been studied extensively, but with a particular focus on their invaded range in Australia (Shine 2010). The published literature we reviewed may not capture the full extent of variation in the life history of either species. We note that ABSTs comprise a species complex (Wogan *et al.* 2016), and that cane toads, as considered in this study, include *R. marina* and *R. horribilis*. Thus, variation in life history characteristics between species is expected, and also among populations of the same species in different locations. Where similarities occur there may be nuanced, consequential differences that have not been documented (Crossland *et al.* 2009).

In addition to a lack of information about potential competitive interactions between ABSTs and cane toads, there are several undocumented areas of ABST ecology, which would be useful to study to enhance response planning for incursions. These include details of spatial ecology, thermal and desiccation thresholds, and diet and habitat of tadpoles and metamorphs. Additionally, there are recorded differences in traits between ABSTs and cane toads identified in the literature, but these traits are strongly influenced by

environmental conditions that could be further explored. This applies to clutch size, egg development rate, maximum densities, rates of spread, and call characteristics.

A detailed understanding of species ecology can inform response management. Knowledge of the extent of dependence of ABSTs on water sources could help predict ABST spread and suggest control measures. For example, cane toad activity during the dry season is restricted to permanent water bodies (Schwarzkopf and Alford 2002; Southwell *et al.* 2017). In arid Western Australia, cane toads can survive a maximum of 5 days without water and move up to 5.35 km during that period (Gregg *et al.* 2019). However, cane toads can alter their behaviour to reduce the effects of desiccation in water-limited environments, for example by finding underground water, burrowing, and remaining inactive (Schwarzkopf and Alford 2002; Bruschi *et al.* 2019). In addition, cane toad amplexus can occur both close to, and distant from water bodies (Bowcock *et al.* 2009). It is unknown how ABSTs respond to arid or water-limited environments, which could affect their distribution in Australia. Understanding these traits could allow for targeted surveillance and response measures.

Thermal thresholds can be used to infer the success of a species in different environments. Cane toad tadpoles cannot develop in water below 16°C, and metamorphs have a lethal maximum temperature of 42°C, which may limit their distribution (Child *et al.* 2008b; Wijethunga *et al.* 2016). However, cane toads have increased cold tolerance following establishment and spread in both Australia and Florida (McCann *et al.* 2014; Mittan and Zamudio 2019). ABSTs occur at a range of elevations and can alter thermal sensitivity based on temperature (i.e. toads from lower elevations have higher thermal optimal temperatures, whereas toads from higher elevations have lower thermal optima (Algiriyage *et al.* 2020)), yet little information exists on the effect of temperature on ABST performance or their development. As such, the influence of exposure to extreme temperatures, such as those found in Australia, on ABST development, behaviour, or potential distribution are not known. The scope for ABSTs to increase cold tolerance in new environments, as cane toads have done, is also unknown. More detailed information on thermal tolerances would allow detailed modelling of survival of incipient populations and potential habitat.

## Conclusion

ABSTs pose a significant biosecurity threat to Australia. Much of the northern coastline, including where border interceptions at ports have been most frequent (Tingley *et al.* 2018), is suitable habitat, and ABSTs potentially have impacts similar to those of cane toads. Should an ABST incursion occur, the invading population will likely encounter an established cane toad population. Because the two species share life history similarities and exhibit similar climatic niches, interspecific competition may affect establishment and impacts of

ABSTs. Comparative investigation of the life histories and functional responses of these two species, undertaken within the native and invaded ranges of ABSTs, would help indicate the likely outcomes of species interactions in the context of an ABST invasion of Australia. Examination of key components of ABST life history, including thermal and desiccation thresholds and spatial and reproductive ecology, will assist in response planning for ABST incursions.

## Supplementary material

Supplementary material is available [online](#).

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**Data availability.** The data that support this study will be shared upon reasonable request to the corresponding author.

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