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Species' traits drive amphibian tolerance to anthropogenic habitat modification

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Abstract

Anthropogenic habitat modification is accelerating, threatening the world's biodiversity. Understanding species' responses to anthropogenic modification is vital for halting species' declines. However, this information is lacking for globally threatened amphibians, informed primarily by small community-level studies. We integrated >126,000 verified citizen science observations of frogs, with a global continuous measure of anthropogenic habitat modification for a continental scale analysis of the effects of habitat modification on frogs. We derived a modification tolerance index—accounting for anthropogenic stressors such as human habitation, agriculture, transport and energy production—for 87 species (36% of all Australian frog species). We used this index to quantify and rank each species' tolerance of anthropogenic habitat modification, then compiled traits of all the frog species and assessed how well these equipped species to tolerate modified habitats. Most of Australia's frog species examined were adversely affected by habitat modification. Habitat specialists and species with large geographic range sizes were the least tolerant of habitat modification. Call dominant frequency, body size, clutch type and calling position (i.e. from vegetation) were also related to tolerance of habitat modification. There is an urgent need for improved consideration of anthropogenic impacts and improved conservation measures to ensure the long-term persistence of frog populations, particularly focused on specialists and species identified as intolerant of modified habitats.

KEYWORDS
amphibian declines, anthropogenic, biodiversity, citizen science, conservation, habitat modification, life history, species traits

1 | INTRODUCTION

Anthropogenic habitat modification adversely impacts global biodiversity. Changed ecosystems can cause population declines, even extinctions (Johnson et al., 2017; Tilman et al., 2017). Habitat conversion, and urbanization in particular, drastically changes species assemblages by clearing, degrading and fragmenting natural habitats; introducing predators, pathogens and invasive species; modulating resources; creating artificial structures; and increasing noise, light and chemical pollution (Alberti, 2015). To persist in

these environments, species must cope with the novel conditions (Sih et al., 2011). Shifts in morphological, behavioural and physiological traits can improve species' survival and reproduction in highly modified landscapes (Sullivan et al., 2017). As urban and agricultural areas, and supporting industries, expand at increasing rates (Liu et al., 2020), understanding species-specific responses to anthropogenic modification is vital for identifying vulnerable species and mitigating risk to biodiversity.

Modified habitats filter species that naturally occur based on their traits, removing species with traits unfit for novel anthropogenically

modified environments (Croci et al., 2008; Webb et al., 2010). For example, species with relatively little behavioural flexibility can disappear from anthropogenically modified habitats (Sih et al., 2011). Contrastingly, species with large residual brain sizes, high fecundity, large breeding ranges and dispersal capacities, high adult survival rates, or adaptations to assist with locomotion can persist in anthropogenically modified habitats (Callaghan, Roberts, et al., 2020; Croci et al., 2008; Moller, 2009; Richardson et al., 2020; Winchell et al., 2016). Consistently, generalists are more successful than specialist species in disturbed environments (Callaghan, Roberts, et al., 2020; Ducatez et al., 2018; Evans et al., 2011; Keinath et al., 2017). A study of terrestrial vertebrate species (25,985) found that urban dwellers occupied a wider niche than urban avoiding species and consequently tolerated a broad range of environmental conditions, including those found in modified urban habitats (Ducatez et al., 2018). Consequently, species' pools within anthropogenically modified habitats are often homogenized, less taxonomically, functionally and phylogenetically diverse, given selection of similar ecological and life history traits (Aronson et al., 2016; Nowakowski et al., 2018). However, our understanding of tolerance of biodiversity to such modified environments is biased towards birds and mammals. For example, Ducatez et al. (2018) considered almost all extant bird and 81% of mammal species, but only 72% of amphibian species; a similar bias exists in other studies (Keinath et al., 2017). There is a significant research gap for amphibians, one of the most threatened vertebrate groups.

Amphibian extinctions are occurring at unprecedented rates, exacerbated by current levels of human land use (Gonzalez-Del-Pliego et al., 2019; Hero & Morrison, 2004). Roads, residential development and other anthropogenic habitat modification reduce species' occurrence and abundance (Anderson, 2019; Gagné & Fahrig, 2010; Villaseñor et al., 2017). Although highly disturbed areas tend to support fewer amphibian species than unmodified areas (Pillsbury & Miller, 2008; Scheffers & Paszkowski, 2011), there is significant co-occurrence of amphibians with modified areas (e.g. cities), highlighting their importance for amphibian conservation (Nori et al., 2018; Westgate et al., 2015). Some urban habitats may even support more threatened species than non-urban habitats (Ives et al., 2016). To make informed conservation decisions with increasing anthropogenic development, two things are needed: (a) an objective classification of a species' ability to persist in anthropogenic environments, providing a continuous ranking from resilient to sensitive species, and (b) an understanding of which ecological and life history traits allow persistence in anthropogenically modified habitats, allowing for trait-based targeted conservation interventions (Scheffers & Paszkowski, 2011).

Phylogeny, geographic range size, elevational range, larval habitat, reproductive mode and generalism moderate amphibian sensitivity to anthropogenic habitat modification (Hirschfeld & Rodel, 2017; Nowakowski et al., 2018; Nowakowski, Watling, et al., 2018). Mobility and extended breeding seasons may also be positively related to modification tolerance (Francesco Ficetola & De Bernardi, 2004; Kruger et al., 2015). In contrast, early breeding activity, short hydroperiods, low heat tolerance and habitat specialism are associated with low tolerance of habitat modification (Kruger et al., 2015; Nowakowski et al.,

2018; Pillsbury & Miller, 2008). Much of our current understanding remains limited by use of disparate, region-specific measures of anthropogenic habitat modification and relatively spatially restricted studies with few species (disproportionately representing pond breeding species), mostly in North America, Europe and other temperate regions (Kaczmarski et al., 2020; Pillsbury & Miller, 2008). Macroecological analyses are needed to understand tolerance associations of amphibians to anthropogenic habitat modification.

Such an approach demands access to taxonomically and geographically comprehensive species' locality data. While these data are difficult to obtain using traditional survey methods, citizen science projects have increasingly provided large volumes of high-quality data, enabling trait-based analyses (Callaghan et al., 2020; Rowley et al., 2019). We aimed to identify ecological and life history traits that allowed frogs to tolerate anthropogenic modification, using continent-wide citizen science data integrated with a global human modification index. We had two main objectives. First, we quantified and ranked anthropogenic habitat modification tolerance among Australian frog species, using this to predict persistence or decline. Second, we analysed which morphological, reproductive and ecological traits mediated species' responses to this habitat modification.

2 | MATERIALS AND METHODS

2.1 | Frog dataset

We compiled frog occurrence data from FrogID, an Australia-wide citizen science project consisting of expert-validated audio recordings of frogs (Rowley et al., 2019). Users submit 20- to 60-second audio recordings of one or more frogs via a smartphone app that collects date, time and location metadata. Experts validate and identify all species calling in recordings. We used data collected between 10 November 2017 (project launch) and 31 March 2020 but excluded recordings where location could not be accurately assigned (3.8%). Duplicate submissions of the same species from the same location (same latitude and longitude to 4 decimal places) were then removed (23.2%) to minimize overrepresentation of individual frogs. We then filtered the data to include only species with >100 observations (98.1%) to represent a greater level of confidence surrounding the species-specific estimates (*sensu* Callaghan, Roberts, et al., 2020). We chose 100 observations as the threshold as a random sampling analysis revealed that variation in species' modification indices was noticeably reduced at ~100 observations (see Figure S3). The final dataset included 87 species (86 native frog species, plus the introduced cane toad, *Rhinella marina*; filtered from 196 species), representing 36% of Australian frog species.

2.2 | Anthropogenic modification index

We used the global human modification (GHM) index (Kennedy et al., 2019) to derive a continuous measure of modification (hereafter 'modification index') for each species. The GHM index ranges

from 0 (low human impact) to 1 (high impact), representing the cumulative impact of five major anthropogenic stressors, including human settlement, agriculture, transport, energy production and electrical infrastructure. The index correlated strongly with other measures of anthropogenic modification, including human population density and VIIRS night-time lights (Figures S1 and S2). We used the latitude and longitude of each FrogID submission and Google Earth Engine (Gorelick et al., 2017) to extract the GHM index within a 1 km buffer of each location, about the spatial scale over which frogs are susceptible to anthropogenic influences (e.g. roads; Villaseñor et al., 2017). Each species had a unique distribution of densities of observations across the anthropogenic modification gradient (e.g. Figure 1). The median value of this distribution was the 'species' anthropogenic modification score'. We also determined a 'geographic range modification score' (Figure 1) for each species, defined as the median GHM value of all observations within the given species' geographic range, that is, all FrogID

records within that species' geographic range, including other species. Species' geographic ranges were obtained from FrogID, which were informed by Atlas of Living Australia records (present and historic occurrence data), modified by expert opinion and FrogID data (Rowley et al., 2019).

We took the difference between the species' median (species' anthropogenic modification score) and the geographic range median (geographic range modification score) to calculate a relative modification index (Figures 2 and 3), our response variable (*sensu* Callaghan et al., 2020). A large modification index indicated a species had a high proportion of its records in human-modified regions within its geographic range, reflecting tolerance of anthropogenic modification. Likewise, a negative modification index denoted a species had a high proportion of its records in relatively unmodified areas (relative to available habitat) within its geographic range, reflecting low tolerance of anthropogenic modification. Our modification index considered that occurrence in anthropogenically modified regions did
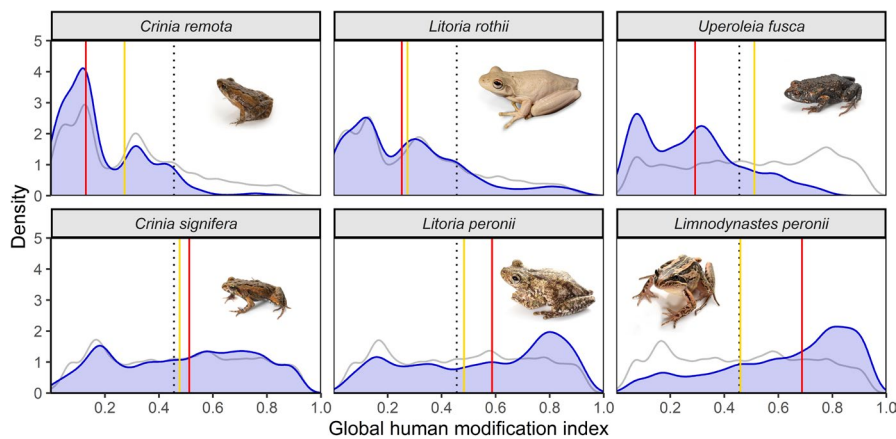

FIGURE 1 Individual density distributions of frog observations (in blue) in relation to the global human modification (GHM) index for six species of Australian frogs, showing median GHM values for each species (species' anthropogenic modification score, red line); median GHM for all the observations (including other species) within the given species' geographic range (geographic range modification score, yellow line; associated density distribution, grey line); and median GHM for all observations of all 87 species analysed (overall modification score, dotted line; see Figure S5 for density distribution). For each species, the difference between the species' anthropogenic modification score and the geographic range modification score was the response variable (i.e. the 'modification index'), representing tolerance of anthropogenic modification. [Photo credits: J.J.L.R.]
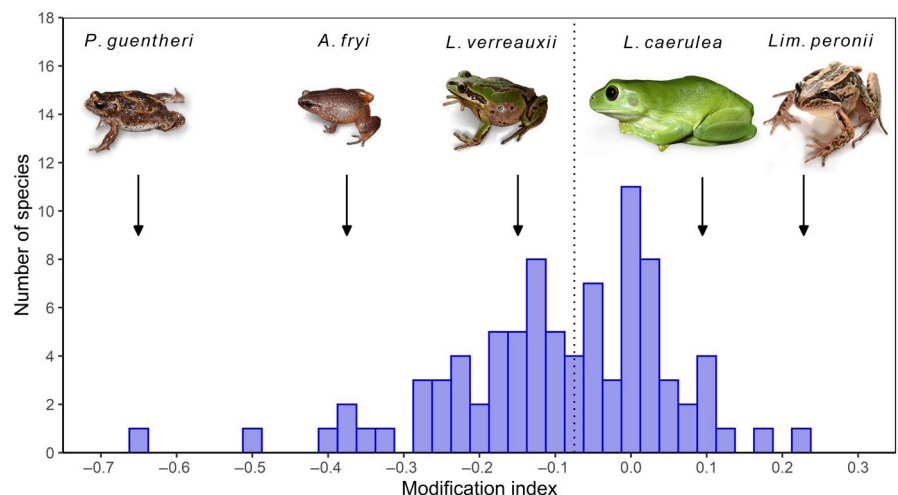

FIGURE 2 Number of frog species (*N* = 87) and their relationships to the anthropogenic modification index, with six example species, indicated by the arrows (median value for all species represented by dotted line). [Photo credits: *Pseudophryne guentheri* and *Austrochaperina fryi*, S. Mahony; *Litoria verreauxii*, *Litoria caerulea* and *Limnodynastes peronii*, J.J.L.R.]
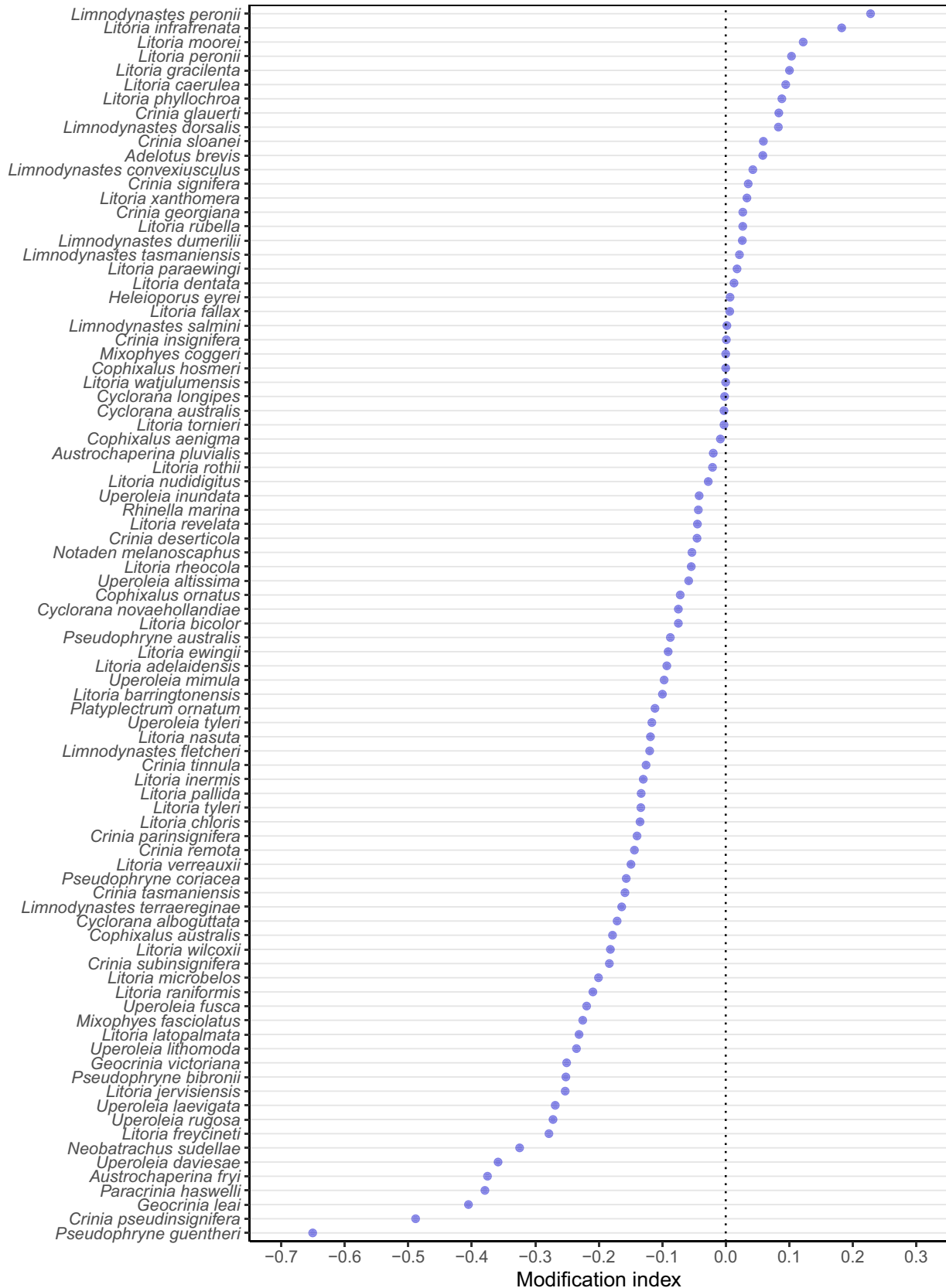
FIGURE 3 Anthropogenic modification index for each of 87 Australian frog species, with an index of 0 representing no difference between the species' anthropogenic modification score (species' median scores) and geographic range modification score (median score across the species' geographic range). A positive modification index indicated occurrence in more modified areas compared to other observations (including other species) within the species' geographic range; a negative index indicated occurrence in relatively less modified areas compared to other observations within the species' geographic range

not necessarily equate to modification tolerance. For example, species may occupy unmodified habitat (e.g. forest fragments) within a matrix of modified habitat, in which case the overall area would be considered 'modified', but the species itself would be considered to occupy unmodified habitat.

Sampling biases are common in citizen science data. In our dataset, urban areas were better sampled compared to remote regions, as contributors typically concentrate around areas with high human density (Callaghan et al., 2020). However, considering all observations, sampling bias across the modification gradient was generally small (Figure S5) and was accounted for because each species' anthropogenic modification index was calculated relative to the observations across its geographic range. Importantly, while disproportionate sampling in human occupied areas may inflate the modification index, each species in the dataset was subject to similar biases (Figure S4), enabling comparisons across species. We tested the sensitivity of species' modification indices to both spatial and intra-annual temporal biases (see Figure S6) present in the FrogID data and found that the indices were robust despite the apparent sampling biases (Figure S7).

2.3 | Ecological and life history traits

For each species in our dataset, we collected ecological and life history traits from published literature, including body size, clutch type, clutch size, ecological group, calling positions, tadpole positions in the water column, range size, climate zones, habitats and call dominant frequency (Table 1). Species' names were updated if necessary, to match the current nomenclature. Traits were analysed based on *a priori* predictions of influence (see Table S1 for predictions and traits), and were either obtained directly from the literature, or were modified or summarized, where appropriate (e.g. to represent various measures of generalism; see details in Table 1). Ecological groups were modified from Murray et al. (2011), based on expert opinion and habitat data associated with FrogID submissions.

As clutch sizes can be highly variable within species, and are relatively infrequently documented, we assigned each species to one of three clutch size categories (small, medium or large), based on maximum reported clutch sizes (Anstis, 2017; Bielby et al., 2008). The limits of each category were determined as the lower (<160) and upper (>875) third quantiles of all available clutch size measurements

TABLE 1 Ecological and life history traits (predictor variables) for 87 Australian frog species (from different sources, superscripts), used in analyses of relationships between species' traits and the anthropogenic modification index. See Table S1 for associated hypotheses

Trait	Description
Life history traits	
Body size[a]	Maximum snout-vent length (mm) of males.
Clutch type[a]	Egg clutches are classified broadly as aquatic: foamy; aquatic: non-foamy; semi-terrestrial: foamy; terrestrial: foamy; or paraviviparous. However, no species in our dataset were paraviviparous.
Clutch size[a,b]	Typical clutch size, classified broadly into three categories: small (<160), medium (160–875) and large (≥876).
Adult habitat	
Ecological group[c]	Ephemeral pond breeders, E; moist bog/soak associated, M; permanent water associated, P; stream associated, S; or terrestrial breeders, T.
Calls from vegetation[a]	Males call from vegetation (yes/no).
Distribution	
Range size	Geographic range size (km^2).
Generalism	
Tadpole generalism[a]	Number of positions in the water column typically occupied by tadpoles (range: 0–3). Possible positions: none, top, middle, bottom.
Climate generalism	Number of climate zones occupied by adult frogs (range: 1–6). There were six climates zones: desert, equatorial, grassland, subtropical, temperate and tropical.
Habitat generalism	The number of land cover classes occupied by adult frogs (range: 1–14) as classified by the global land cover map (ESA 2010 and UCLouvain). There are 22 land cover classes in total.
Number of calling positions[a]	Number of calling positions (range: 1–3). Possible positions: above ground; ground/below ground; above water; in water.
Other	
Call dominant frequency[d]	Dominant frequency (Hz) of male advertisement calls. We focused on dominant frequency as it is easily quantifiable and less labile (e.g. in response to ambient temperature) than other calling traits (Tonini et al., 2020).

[a]Anstis (2017).

[b]Bielby et al. (2008).

[c]Modified from Murray et al. (2011).

[d]Tonini et al. (2020). Where dominant frequency data were not available for a species, we determined the mean dominant frequency from five randomly selected FrogID recordings for that species, using the sound analysis software Raven Pro 1.5.0 (FFT = 512, window = Hann, overlap = 50%; Bioacoustics Research Program, 2017).

from frog species in Australia. Where this information was missing, a category was assigned, based on estimates of clutch size, informed by published literature and closely related species. We calculated various measures of generalism, accounting for both adult and tadpole life stages. These were created on the basis that generalist species typically occupy a wide range of environmental conditions, climates or habitats (Ducatez et al., 2018). The habitat generalism predictor variable was obtained by counting the number of land cover classes (*N* = 22) occupied by each species, from a global land cover map (GlobCover; ESA 2010 and UCLouvain), using FrogID location records for the species and Google Earth Engine. Likewise, the climate generalism predictor variable was obtained by assigning each FrogID observation to one of six climates zones (desert, equatorial, grassland, subtropical, temperate and tropical) and tallying the total number of zones occupied by each species. All 87 species analysed had complete data for all traits, but we removed the moaning frog (*Heleioporus eyrei*) from further statistical analyses (i.e. it was retained in our study only for calculating modification scores for Objective 1) because it was the only species in the 'semi-terrestrial foamy' clutch category.

2.4 | Statistical analyses

Analyses were conducted in R version 3.6.2 (R Core Team, 2019). To determine whether species' responses to modification were related to evolutionary relationships, we tested for phylogenetic signal in our modification index, using a published amphibian phylogenetic tree (Jetz & Pyron, 2019). We used the 'phylosignal' package (Keck et al., 2016) to compute phylogenetic signal statistics, employing all available indices (Abouheif's Cmean, Moran's I, Bloomberg's K and K*, and Pagel's Lambda), due to their variable performance under different conditions (Münkemüller et al., 2012). As the indices differed in their assessment of the importance of phylogeny on species' responses to modification (see results), we constructed both phylogenetically controlled and non-phylogenetically controlled linear regression models. We first examined our ecological and life history traits for multicollinearity (Figure S11) using the 'corrplot' package (Wei & Simko, 2017) and generalized variance inflation factors (GVIFs; 'car' package, Fox & Weisberg, 2019). As multicollinearity was minimal (GVIF ≤2; Table S2), all traits were retained for modelling. Continuous and binary predictor variables were standardized using the 'arm' package (Gelman & Su, 2018). Models were weighted by the number of observations of each species, capped at 1000, to ensure that species with more observations, likely to have the most reliable modification index, were given more weight.

We were interested in the independent relationships between our predicted traits (Table 1) and anthropogenic modification tolerance and so we first ran multiple individual linear models to test the strength of relationships between each trait (predictor variable) and anthropogenic modification tolerance (response variable). We then tested which traits were most associated with anthropogenic modification tolerance, accounting for the other traits, using a multiple linear regression model. Because of multiple competing hypotheses and the lack of generally consistent results previously reported in the trait-based literature, we used a model-averaging approach. Model averaging accounts for model selection uncertainty, and where multiple models are similarly supported by data, averaging across the top model set can provide robust parameter estimates (Grueber et al., 2011; Hobbs & Hilborn, 2006). We used the dredge function ('MuMIn' package; Barton, 2019) to derive all possible sub-models (*N* = 2048) from a global model of the 11 predictor traits. This approach allowed any combination of traits to be predictor variables and avoided over-fitting. We then determined weighted average parameter estimates and errors across the top model set (ΔAICc < 4), using the conditional average, as we wanted to evaluate all potentially important traits and expected some to have relatively weak effects (Grueber et al., 2011). All models were fitted using a Gaussian distribution, confirmed as the best distribution by checking model assumptions.

The same approach (i.e. individual linear models and a model-averaged multiple linear regression model), response and predictor variables were retained for the phylogenetically controlled models. We used the 'phylolm' package (Ho & Ane, 2014) to fit phylogenetic linear regression models, where the likelihood was linear in the number of tips in the tree.

2.5 | Data availability

The complete raw dataset is not fully available, due to sensitivities in relation to locations of rare or threatened species and citizen scientist information (Rowley & Callaghan, 2020). However, the data, with sensitive species' localities removed or buffered, are made available annually (Rowley & Callaghan, 2020). The processed species' anthropogenic modification indices and the code to reproduce our results are available in a Zenodo repository at http://doi.org/10.5281/zenodo.4638313.

3 | RESULTS

Our analyses included a total of 126,182 observations for the 87 species, averaging 1892 ± 3543 (±*SD*) observations per species. The common eastern froglet (*Crinia signifera*) was the most frequently recorded species (*N* = 21,042), whereas the common mist frog (*Litoria rheocola*) and the salmon-striped frog (*Limnodynastes salmini*) were least recorded (both *N* = 106). Most species (61/87, 70%) showed a negative response to anthropogenic habitat modification (index <0; Figure 3). The average modification index was −0.095 ± 0.149 (±*SD*). The highest indices were recorded in the striped marsh frog (*Limnodynastes peronii* = 0.228), white-lipped tree frog (*Litoria infrafrenata* = 0.183) and motorbike frog (*Litoria moorei* = 0.122), indicating a high tolerance to anthropogenic modification. Conversely, the

TABLE 2 Summaries (estimates; *SE*; *z* scores; *p*-values (bold for significant); and sum of model weights, sw) of relationships between ecological and life history traits and species' anthropogenic modification index for four different modelling approaches: phylogenetically controlled (phylolm) or non-phylogenetically controlled (lm), multiple linear regression with model averaging, or single regressions for each trait. For multiple linear regressions, the intercept was the reference level for any categorical traits (e.g. clutch type; clutch size; ecological group; calling position: calls from vegetation)

| Term	Multiple regression (lm)					Multiple regression (phylolm)					Single regression (lm)				Single regression (phylolm)			
	Estimate	SE	z	p-value	sw	Estimate	SE	z	p-value	sw	Estimate	SE	t	p-value	Estimate	SE	t	p-value
(Intercept)	-0.01	0.04	0.33	0.741	–	-0.11	0.21	0.52	0.606	–	–	–	–	–	–	–	–	–
log(Body size)	0.06	0.04	1.80	0.072	0.60	-0.18	0.08	2.16	**0.031**	0.71	0.09	0.03	3.30	**0.001**	-0.08	0.07	-1.18	0.241
Clutch type: aquatic foamy	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Clutch type: aquatic non-foamy	-0.04	0.04	0.92	0.356	1.00	-0.16	0.23	0.71	0.476	0.04	-0.07	0.04	-1.96	0.053	-0.22	0.25	-0.87	0.387
Clutch type: terrestrial non-foamy	-0.21	0.07	3.02	**0.003**	1.00	-0.28	0.26	1.08	0.28	0.04	-0.23	0.06	-3.75	**<0.001**	-0.27	0.28	-0.97	0.335
Clutch size: small	-0.01	0.05	0.17	0.866	0.35	–	–	–	–	–	-0.08	0.04	-1.73	0.088	0.15	0.07	1.98	0.051
Clutch size: medium	-0.06	0.04	1.69	0.091	0.35	–	–	–	–	–	-0.09	0.03	-2.87	**0.005**	0.06	0.05	1.30	0.195
Clutch size: large	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ecological group: E	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ecological group: E/P	0.08	0.04	1.93	0.053	0.09	–	–	–	–	–	0.07	0.04	1.57	0.119	-0.03	0.04	-0.84	0.404
Ecological group: P	0.01	0.05	0.14	0.888	0.09	–	–	–	–	–	0.06	0.05	1.08	0.284	0.05	0.06	0.71	0.481
Ecological group: S	0.17	0.08	2.22	**0.027**	0.09	–	–	–	–	–	0.13	0.09	1.50	0.139	0.07	0.14	0.53	0.600
Ecological group: T	0.22	0.11	2.08	**0.038**	0.09	–	–	–	–	–	0.02	0.1	0.15	0.878	0.18	0.21	0.83	0.409
Calls from vegetation	0.07	0.03	2.37	**0.018**	0.91	0.06	0.05	1.32	0.186	0.42	0.10	0.03	3.08	**0.003**	0.08	0.05	1.59	0.116
log(Range size)	-0.16	0.05	3.18	**0.001**	1.00	-0.18	0.05	3.6	**<0.001**	1.00	0.01	0.04	0.21	0.835	-0.08	0.04	-2.45	**0.016**
Tadpole generalism	0.05	0.04	1.05	0.294	0.28	0.04	0.05	0.85	0.395	0.23	0.06	0.03	1.92	0.058	0.03	0.05	0.70	0.484
Climate generalism	0.09	0.04	2.38	**0.017**	0.90	0.04	0.06	0.64	0.520	0.19	0.04	0.03	1.58	0.117	-0.02	0.03	-0.48	0.633
Habitat generalism	0.07	0.05	1.36	0.175	0.40	0.09	0.04	2.38	**0.017**	0.96	0.09	0.04	2.43	**0.017**	0.00	0.03	-0.05	0.961
Number of calling positions	0.02	0.03	0.62	0.538	0.16	-0.05	0.03	1.48	0.138	0.46	0.03	0.03	1.13	0.263	-0.01	0.03	-0.37	0.713
Call dominant frequency	-0.06	0.04	1.49	0.137	0.41	-0.15	0.07	2.12	**0.034**	0.81	-0.08	0.03	-2.70	**0.008**	-0.06	0.06	-1.09	0.280
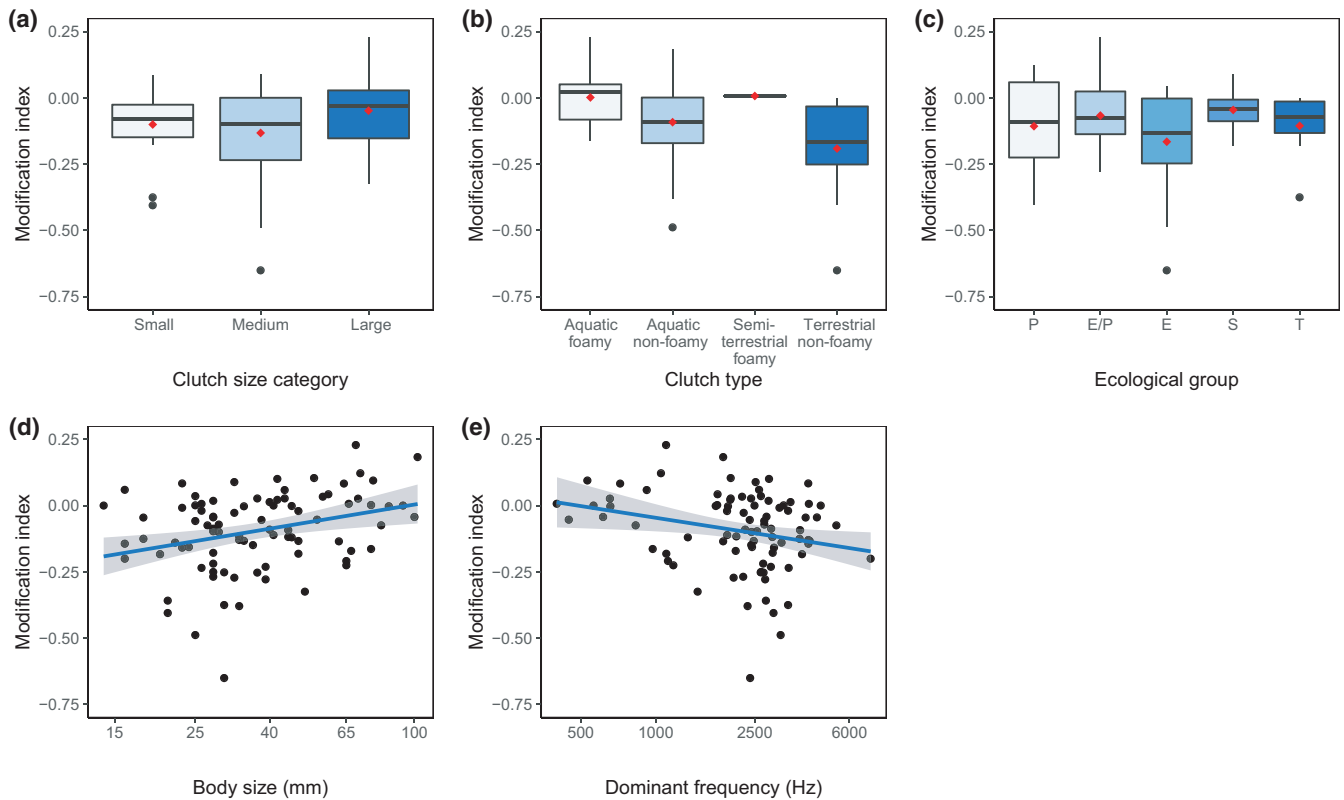
FIGURE 4 Relationships between the anthropogenic modification index and ecological and life history traits. Boxplots of categorical variables (a–c) depict medians, interquartile ranges and full ranges, overlaid with the mean (red diamonds): (a) clutch size category, small (<160), medium (160–875), large (≥876); (b) clutch type (*Heleioporus eyrei* in the 'semi-terrestrial foamy' clutch type category was removed from statistical analyses); (c) ecological group, P = permanent water associated, P/E = permanent water and ephemeral pond breeder; E = ephemeral pond breeder, S = stream associated, T = terrestrial breeder; (d) male body size (mm); and (e) call dominant frequency (Hz)

crawling toadlet (*Pseudophryne guentheri* = −0.651), bleating froglet (*Crinia pseudinsignifera* = −0.489) and ticking frog (*Geocrinia leai* = −0.405) were the least tolerant of anthropogenic modification.

When testing for a phylogenetic signal in our modification index, we found some evidence—with three significant indices (Cmean, I and Lambda)—that species' responses to anthropogenic modification were phylogenetically related (Cmean statistic = 0.199, $p = 0.002$; I statistic = 0.048, $p = 0.018$; K statistic = 0.128, $p = 0.179$; K* statistic = 0.143, $p = 0.148$; Lambda statistic = 0.308; $p = 0.018$). When traits were assessed independently in non-phylogenetically controlled linear models, body size was significantly positively associated, and call dominant frequency was significantly negatively associated, with species' tolerance of anthropogenic modification (single regression, lm, Table 2; Figure 4d,e). Habitat generalists and species that called from vegetation were more tolerant of anthropogenically modified environments than specialists or species that did not call from vegetation. Species with large clutches (≥876 eggs) were more tolerant of anthropogenic modification than species with small- or medium-sized clutches (Figure 4a), but species with small clutches (<160 eggs) were more tolerant of anthropogenic modification than species with medium-sized clutches (160–875 eggs). Furthermore, species with terrestrial non-foamy clutches were less tolerant of anthropogenic modification than species that laid

their eggs in water (Figure 4b). There were no other relationships between remaining traits, including ecological grouping (Figure 4c), and tolerance to anthropogenic modification. However, when traits were assessed using the same modelling approach, but controlling for phylogeny, geographic range size was significantly negatively associated with modification tolerance; no other traits were significant (single regression, phylolm, Table 2).

When assessing traits using non-phylogenetically controlled multiple linear regression models, the 'best model' (lowest AICc) included clutch type, calling from vegetation (yes/no), climate generalism, body size and geographic range size; all were statistically significant (Table S5). Climate generalism and body size were positively related to tolerance of anthropogenic modification, and species that called from vegetation were more tolerant than those that did not. Geographic range size was negatively related to tolerance, and species with terrestrial non-foamy clutches were less tolerant of anthropogenic modification than species with aquatic clutches. The results were similar when model averaging across the 'top model set', which included 36 models (Table S3). Geographic range size and terrestrial non-foamy clutches were present in each of the top models and were significantly negatively related to tolerance of anthropogenic modification, after accounting for other traits (multiple regression, lm, Table 2; Figure 5). Conversely, climate

generalism and calling from vegetation positively indicated tolerance to anthropogenic modification. Ecological groupings were also significantly positively associated with tolerance of anthropogenic modification (but presented in only five of 36 top models); stream-associated and terrestrial species were more tolerant of anthropogenic modification than species breeding in ephemeral or permanent ponds.

When assessing traits using phylogenetically controlled multiple linear regression models, the 'best model' in terms of AICc included the number of calling positions, habitat generalism, body size, call dominant frequency and geographic range size (Table S8). Habitat generalism was significantly positively associated with tolerance of anthropogenic modification. Contrastingly, body size, call dominant frequency and geographic range size were all significantly negatively associated with tolerance. When the top 30 models (i.e. 'top model set', Table S6) were modelled averaged, the same traits were statistically significant, and the same trends were observed (multiple regression, phylolm, Table 2). Notably, geographic range size, present in all top models, was strongly negatively associated with tolerance of anthropogenic modification, but clutch size and ecological group

were relatively unimportant after accounting for shared evolutionary history; both were absent from the top model set.

Across both phylogenetically controlled and non-phylogenetically controlled models, the strongest and most consistent relationships were for geographic range size and generalism (habitat and climate generalism), respectively related to intolerance and tolerance of anthropogenic modification. Interestingly, body size was contrastingly related to tolerance of anthropogenic modification in non-phylogenetically controlled models but related to intolerance of anthropogenic modification in phylogenetically controlled models (Figure 5).

4 | DISCUSSION

Anthropogenic habitat modification is a leading cause of global frog declines (Hayes et al., 2010). Mitigating these declines relies on understanding how frogs respond to modified environments. We integrated a continuous measure of anthropogenic habitat modification with citizen science data to derive the most
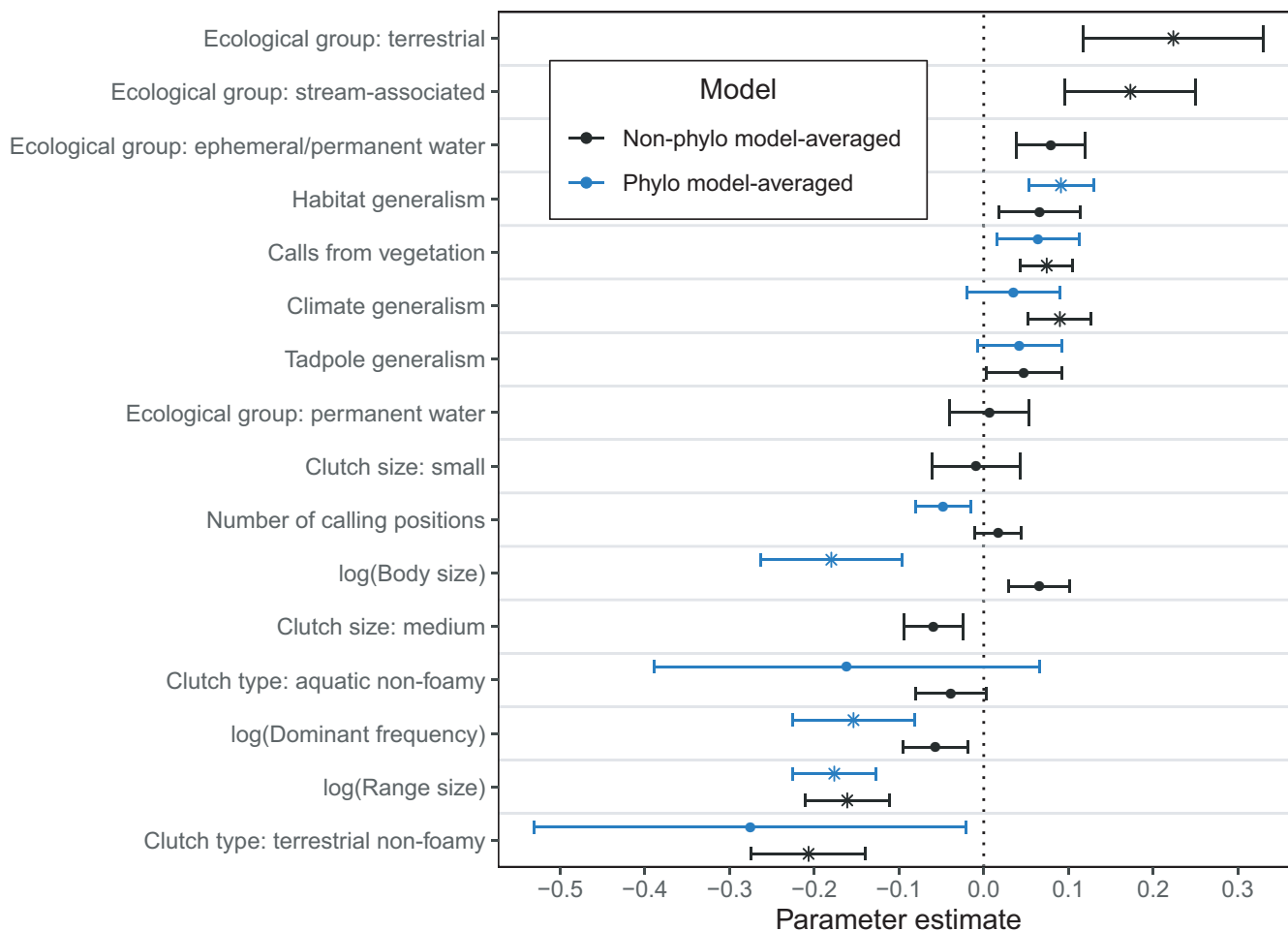

FIGURE 5 Mean (±SE) standardized parameter estimates for predicted ecological and life history traits for the model-averaged non-phylogenetic and phylogenetically controlled top model sets (* indicate statistically significant traits, p < 0.05). Absent traits from the top model set did not have associated parameter estimates

taxonomically comprehensive analysis of modification tolerance among Australian frogs to date. Our continental scale analysis revealed that 70% of the 87 assessed Australian frog species (one introduced) were intolerant of anthropogenic modification. Species tolerant of anthropogenic modification were typically generalists, with small geographic ranges, and low dominant frequency calls. At the macroecological level, generalists, species with wide niches and broad climatic and environmental tolerances, fare better than specialists in anthropogenically modified environments (Callaghan, Roberts, et al., 2020; Henle et al., 2004; Keinath et al., 2017). There was little evidence to support the hypotheses that large geographic range size (Nowakowski, Watling, et al., 2018) and high acoustic frequencies (Parris et al., 2009; Roca et al., 2016) buffered effects of anthropogenic modification. A species' degree of specialism therefore remains one of few consistent and useful markers of persistence in anthropogenic environments. The other traits we tested varied in their ability to explain species' responses to anthropogenic modification.

Increasing geographic range size in frogs did not lead to increasing tolerance to modification, after accounting for other traits, as might be predicted, given amphibian declines are often apparent among species with small geographic range sizes (Hero et al., 2005; Murray et al., 2011; Sodhi et al., 2008). Possibly, this is because trait-based studies of declines are typically general and some traits may be associated with specific threats (e.g. chytrid infection) with little direct relationship with modification tolerance (Bielby et al., 2008; Murray et al., 2011). Range-restricted species are thought to be intolerant of habitat modification due to their narrow niches (Nowakowski, Watling, et al., 2018), but controlling for specialism, we found that species with larger geographic ranges were less tolerant of anthropogenic modification than species with smaller geographic ranges. However, our result may have reflected some biases in the dataset, given range-restricted species were underrepresented (i.e. many were removed from analyses due to insufficient observations). Importantly, our result does not suggest that range-restricted species are tolerant of anthropogenic modification. Since range-restricted species (e.g. *Cophixalus aenigma* and *C. hosmeri*) typically experienced less variation in the intensity of anthropogenic modification across their geographic range compared to wide-ranging species, their anthropogenic modification index tended to shrink towards zero (a neutral response to modification). To better understand how these species are responding to habitat modification, smaller scale studies focussing on the behaviour and population trends of these species are necessary.

Large body size is also commonly associated with amphibian declines (Lips et al., 2003; Sodhi et al., 2008), albeit inconsistently (Callaghan et al., 2020), as we found. Large species were more tolerant of anthropogenic habitat modification than small species when body size was examined alone in non-phylogenetic models, but larger species were more intolerant after controlling for phylogeny and other ecological and life history traits. These contrasting results may be driven by separate processes. First, body size is positively correlated with dispersal ability, advantaging larger, more mobile species in

the acquisition of resources in modified and fragmented landscapes (Nowakowski et al., 2018). Second, large body size is often associated with a slow life history (long lifespan, delayed maturity), reflected in slow population recovery after environmental disturbances (Olden et al., 2008). Tolerant species also displayed low frequency calls, partly driven by body size. Although anthropogenically modified habitats can be loud, species with low frequency calls (similar acoustic spectrum to traffic noise) can still tolerate these environments. Species that called from vegetation were generally modification tolerant, while those with terrestrial non-foamy clutches were intolerant. Species with terrestrial clutches often depend on forest resources (e.g. moist leaf litter) for egg laying and may not persist in anthropogenically modified habitats with fewer of these resources (Nowakowski, Watling, et al., 2018). This indicates that frog diversity could be supported through two complementary strategies: (a) preserving natural habitat; and (b) creating urban greenspaces and 'frog-friendly' gardens (Villaseñor et al., 2017; Westgate et al., 2015).

Human activities can impose strong selective pressures on species' traits (Alberti, 2015; Sullivan et al., 2017). Morphological and behavioural trait changes can arise quickly and can enable greater persistence in modified habitats (Sullivan et al., 2017). Trait changes that improve locomotion are common (e.g. urban lizards evolving longer limbs and more subdigital scales, Winchell et al., 2016; birds in fragmented habitats evolving increasingly pointed wings, Desrochers, 2010). In Australia, morphological and behavioural trait changes in introduced cane toads (*Rhinella marina*), including longer legs, have facilitated their rapid range expansion (Phillips et al., 2006; Urban et al., 2007), but it remains to be seen whether these traits similarly confer tolerance to anthropogenically modified habitats. Here, the modification index of the cane toad (the only introduced frog species in Australia and in our dataset) was unextraordinary relative to the native species and indicated a negative response to anthropogenic habitat modification. Results of the trait-based analyses were also unchanged when only native species were considered (Figure S12). However, a larger dataset, compiling data from other regions with more introduced species, is necessary to determine whether they generally respond differently to native species.

Although we provide some generalized trait-based patterns of amphibian responses to habitat modification, it is important to consider species-specific responses in conservation planning. Species with a positive anthropogenic modification index that are also commonly recorded and broadly distributed across their range are probably tolerant of modified habitats and may even prefer them to undisturbed habitats. Indeed, many of these species, including *Limnodynastes peronii*, *Litoria infrafrenata* and *Litoria moorei*, were frequently recorded in suburban backyards and can tolerate a range of disturbances (Schell & Burgin, 2003; Villaseñor et al., 2017). Several have successfully formed breeding populations in towns outside their native range (*Litoria fallax*, *Litoria gracilenta*, *Litoria rubella*), following human transport (Rowley et al., 2019). Despite this, 70% of species (61/87) had a negative anthropogenic modification index, highlighting adverse impacts of human habitat alteration on

Australian frogs. Habitat loss is clearly a primary threat to biodiversity (Hayes et al., 2010). This negatively affected proportion of species is comparable to other studies (81% of species, Nowakowski et al., 2018). Furthermore, our estimate was probably conservative, given our anthropogenic modification index likely underestimated the impacts of other direct and indirect anthropogenic modifications of habitat such as climate change, introduced species and water resource development. Moreover, many of the remaining 153 unreported Australian species are range-restricted habitat specialists and probably intolerant of anthropogenic changes.

Our modification index reflected a broad range of anthropogenic influences (e.g. buildings, roads, electrical infrastructure and agricultural practices), making it useful for assessing whether urban expansion projects or land use changes will negatively affect frogs. This needs to be combined with an assessment of each species' ecology and population trends, particularly for threatened or infrequently recorded species. For example, the threatened Sloane's froglet (*Crinia sloanei*) was deemed tolerant of anthropogenic modification but this probably reflected bias, given recordings predominantly came from targeted surveys in a small number of suburban sites where the species persists, within a much larger presumptive range (Knight, 2014). Similarly, the green tree frog (*Litoria caerulea*) was assessed as tolerant of anthropogenic modification and was frequently recorded in suburban areas but has recently declined significantly across the Sydney region (Rowley et al., 2019). This reinforces the importance of conserving most Australian frogs, including those presented here with a high modification index, to prevent ongoing declines in the Anthropocene. If citizen science projects can be sustained long term, it may be possible to use time series of global remote sensing datasets (e.g. VIIRS night-time lights) to track temporal trends in species' anthropogenic modification index, including shifts away from or towards modified areas. Continuous modification indices are ideal for this as they provide varying degrees of tolerance to anthropogenic modification, comparable among species, including different taxa across the world (Callaghan, Roberts, et al., 2020; Evans et al., 2011).

Citizen science data were used to assess species' tolerance to anthropogenic habitat modification, identifying which species could persist and which are most at risk, in an increasingly anthropogenic world. With more data, our analyses can be updated for the remaining Australian frog species, increasing understanding of frog responses to anthropogenic modification. In particular, there is opportunity to reduce spatial and temporal sampling biases and improve the breadth of data by encouraging greater citizen scientist participation in rural and regional areas, and in autumn and winter (in areas of Australia where frogs call year-round). Future research can also explore methods to account for error associated with sampling biases in citizen science datasets. Nonetheless, frog species which are specialists and those with large range sizes seem to be the most intolerant of anthropogenic habitat modification. Our findings strongly suggest that most Australian frog species are intolerant of anthropogenic habitat modification, highlighting the need to prioritize them in urban planning and conservation decisions to ensure their long-term persistence.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.