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Species' traits drive amphibian tolerance to anthropogenic habitat modification

Running title: Amphibian tolerance to 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 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: habitat modification, anthropogenic, species traits, life history, citizen science, amphibian declines, biodiversity, conservation

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 urbanisation 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, Ferrari, & Harris, 2011). Morphological, behavioural, and physiological traits can improve species' survival and reproduction in highly modified landscapes (Sullivan, Bird, & Perry, 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, Butet, & Clergeau, 2008; Webb, Hoeting, Ames, Pyne, & LeRoy Poff, 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, and high adult survival rates, such as in birds (Callaghan et al., 2019; Croci et al., 2008; Moller, 2009), can persist in anthropogenically modified habitats. Consistently, generalists are more successful than specialist species in disturbed environments (Callaghan et al., 2019; Ducatez, Sayol, Sol, & Lefebvre, 2018; Evans, Chamberlain, Hatchwell, Gregory, & Gaston, 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, Frishkoff, Thompson, Smith, & Todd, 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, Driscoll, Gibbons, Calhoun, & Lindenmayer, 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, Villalobos, & Loyola, 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: (1) an objective classification of a species' ability to persist in anthropogenic environments, providing a continuous ranking from resilient to sensitive species, and (2) 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, Frishkoff, et al., 2018; Nowakowski, Thompson, Donnelly, & Todd, 2017). Mobility and extended breeding seasons may also be positively related to modification tolerance (Francesco Ficetola & De Bernardi, 2004; Kruger, Hamer, & Du Preez, 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, Watling, 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, Benedetti, & Morelli, 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 this data is difficult to obtain using traditional survey methods, citizen science projects have increasingly provided large volumes of high-quality data, enabling trait-based analyses (Callaghan, Roberts, 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.

Methods

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 20-60 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 minimise 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 et al., 2019). The final dataset included 87 species (86 native frogs, plus the introduced cane toad, *Rhinella marina*), representing 36% of Australian frog species.

Anthropogenic modification index

We used the global human modification (GHM) index (Kennedy, Oakleaf, Theobald, Baruch-Mordo, & Kiesecker, 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 (Figure S1, Figure 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 1km buffer of each location, about the vulnerability sized area in which frogs are susceptible to anthropogenic influences (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, i.e., 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 (Figure 2, Figure 3), our response variable (*sensu* Callaghan, Benedetti, Wilshire, & Morelli, 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 not necessarily equate to modification tolerance. For example, a species' geographic range may have undergone recent modification, with the species persisting only in remaining unmodified areas (e.g., forest remnants), within their otherwise modified geographic range.

Spatial biases are common in citizen science datasets. In our dataset, urban areas were better sampled than remote regions, as contributors typically concentrate around areas with high human density (Callaghan, Roberts, et al., 2020). This sampling bias 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, enabling comparisons across species.

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 summarised, where appropriate (e.g., to represent various measures of generalism; see details in Table 1). Ecological groups were modified from Murray, Rosauer, McCallum, and Skerratt (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, Cooper, Cunningham, Garner, & Purvis, 2008). The limits of each category were determined as the lower (<160) and upper (>875) third quantiles of all available clutch size measurements 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. 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 location records for the species and Google Earth Engine. 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.

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, Rimet, Bouchez, & Franc, 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 multi-collinearity (Figure S6) using the ‘corrplot’ package (Wei & Simko, 2017) and generalised variance inflation factors (GVIF; ‘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 standardised 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, Nakagawa, Laws, & Jamieson, 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.

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

Results

Our analyses included a total of 126,182 observations for the 87 species, averaging 1,892 ± 3,543 (± s.d.) 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 (± s.d.). 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 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-value = 0.002; I statistic = 0.048, p-value = 0.018; K statistic = 0.128, p-value=0.179; K* statistic = 0.143, p-value = 0.148; Lambda statistic = 0.308; p-value = 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 4). 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 4), 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. There were no other relationships between remaining traits, including ecological grouping, 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 out 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).

Discussion

Anthropogenic habitat modification is a leading cause of global frog declines (Hayes, Falso, Gallipeau, & Stice, 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 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 et al., 2019; Henle, Davies, Kleyer, Margules, & Settele, 2004; Keinath et al., 2017). There was little evidence to support the hypotheses that large geographic range size (Nowakowski et al., 2017) and high acoustic frequencies (Parris, Velik-Lord, & North, 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, Williams, & Magnusson, 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 et al., 2017), 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). Our result does not suggest that range-restricted species are tolerant of anthropogenic modification. Since range-restricted species 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).

Large body size is also commonly associated with amphibian declines (Lips, Reeve, & Witters, 2003; Sodhi et al., 2008), albeit inconsistently (Cooper, Bielby, Thomas, & Purvis, 2008), 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 (Ockinger et al., 2010). 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, Poff, & Bestgen, 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 et al., 2017). This indicates that frog diversity could be supported through two complementary strategies: 1) preserving natural habitat; and 2) creating urban greenspaces and 'frog-friendly' gardens (Villaseñor et al., 2017; Westgate et al., 2015).

Although we provide some generalised 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, Frishkoff, et al., 2018). Further, 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 et al., 2019; Evans et al., 2011).

Citizen science data was 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. 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 prioritise them in urban planning and conservation decisions to ensure their long-term persistence.

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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[1]	Maximum snout-vent length (mm) of males.
Clutch type[1]	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[1, 2]	Typical clutch size, classified broadly into 3 categories: small (<160), medium (160-875) or large (≥876).
Adult habitat	
Ecological group[3]	Ephemeral pond breeders, E; moist bog/soak associated, M; permanent water associated, P; stream associated, S; or terrestrial breeders, T.
Calls from vegetation[1]	Males call from vegetation (yes/no).
Distribution	
Range size	Geographic range size (km^2).
Generalism	
Tadpole generalism[1]	Number of positions in the water column 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 6 climates zones: desert, equatorial, grassland, subtropical, temperate, 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[1]	Number of calling positions (range: 1-3). Possible positions: above ground; ground/below ground; above water; in water.
Other	
Call dominant frequency[4]	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).

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[1] Anstis (2017).

[2] Bielby et al. (2008).

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

[4] 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).

Table 2. Summaries (estimates; standard error; 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).

	Multiple regression (lm)					Multiple regression (phylolm)					Single regression (lm)				Single regression (phylolm)			
Term	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

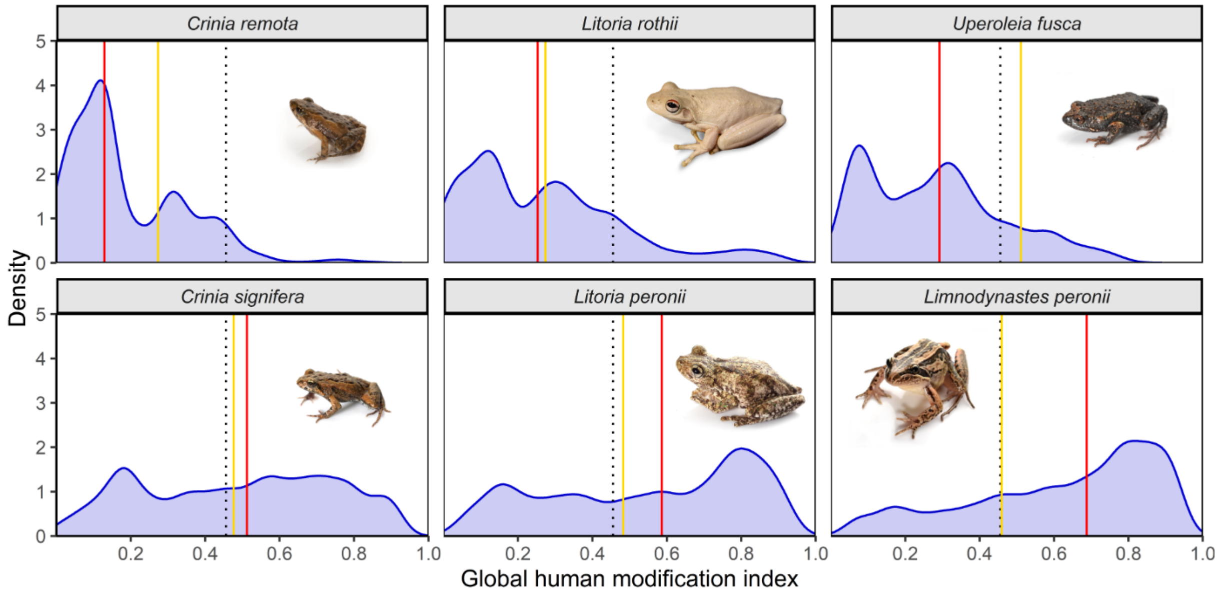


Figure 1. Individual density distributions of frog observations in relation to the global human modification index (GHM) for 6 species of Australian frogs, showing median GHM values for each species (species' anthropogenic modification score, red line); median GHM for all the observations (including other species) within the given species' geographic range (geographic range modification score, yellow line); and median GHM for all observations of all 87 species analysed (overall modification score, dotted line). 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.]

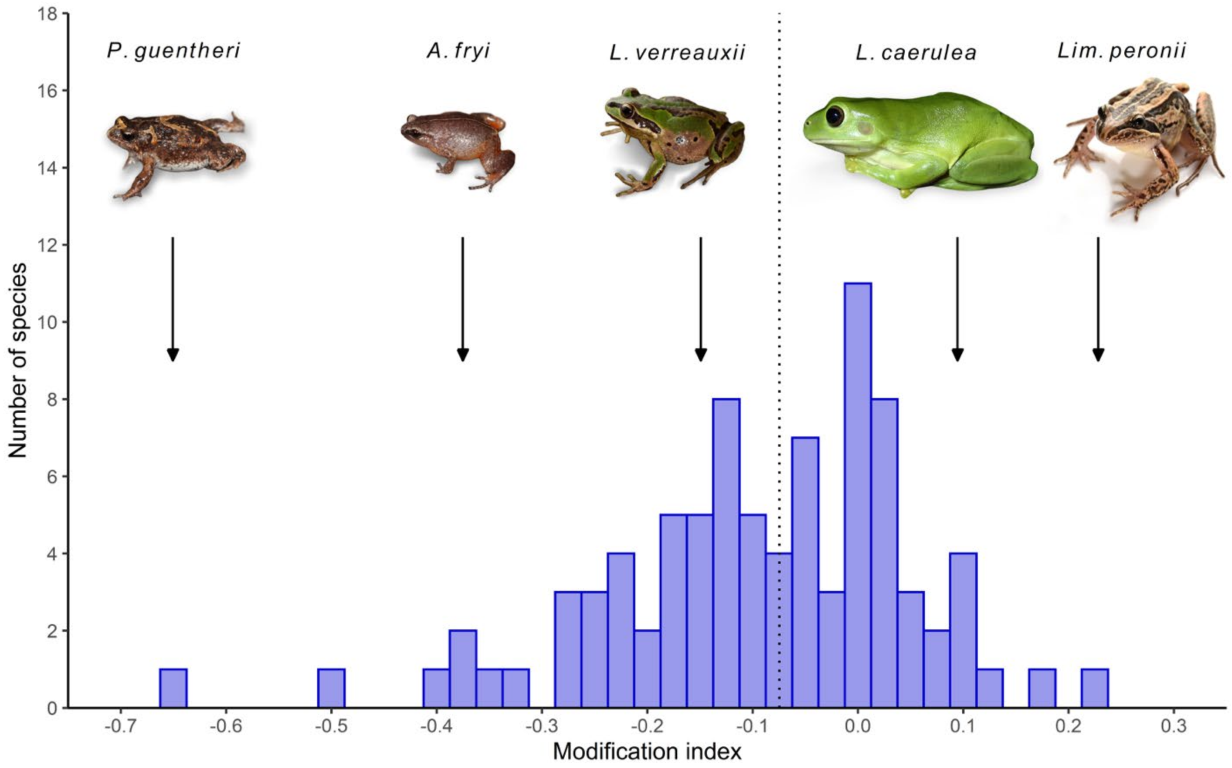


Figure 2. Number of frog species (N = 87) and their relationships to the anthropogenic modification index, with six example species, indicated by the arrows (median value for all species represented by dotted line). [Photo credits: *Pseudophryne guentheri* and *Austrochaperina fryi*, S. Mahony; *Litoria verreauxii*, *Litoria caerulea*, and *Limnodynastes peronii*, J.J.L.R.]

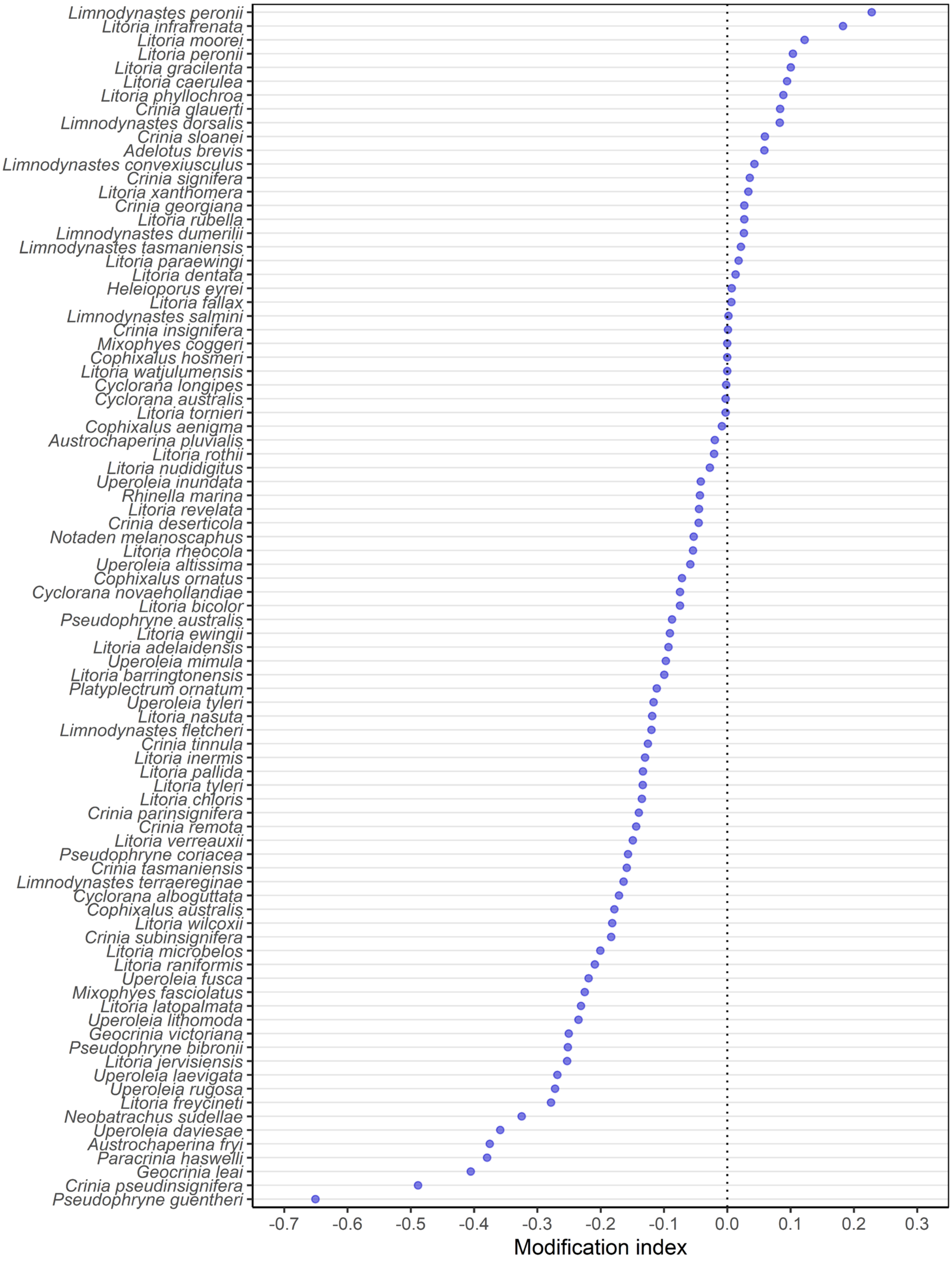


Figure 3. Anthropogenic modification index for each of 87 Australian frog species, with an index of 0 representing no difference between the species' anthropogenic modification score (species' median scores) and geographic range modification score (median score across the

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.

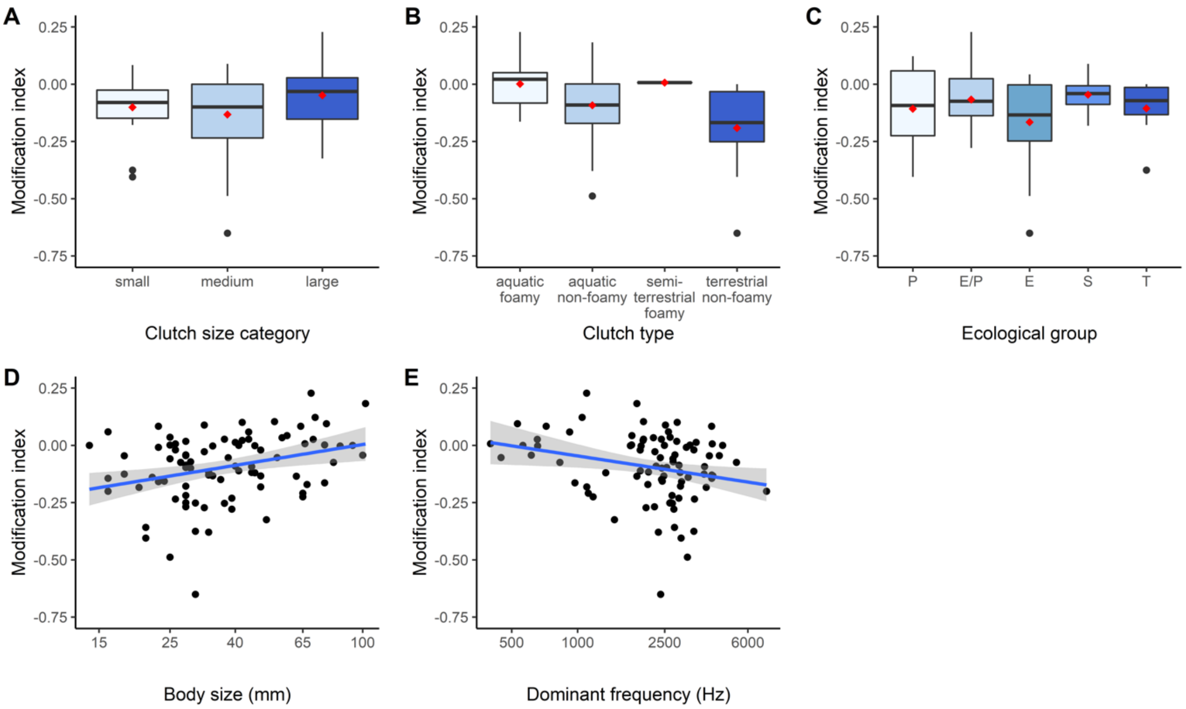


Figure 4. Relationships between the anthropogenic modification index and ecological and life history traits. Boxplots of categorical variables (A-C) depict medians, interquartile ranges, and full ranges, overlaid with the mean (red diamonds): (A) clutch size category, small (<160), medium (160-875), 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).

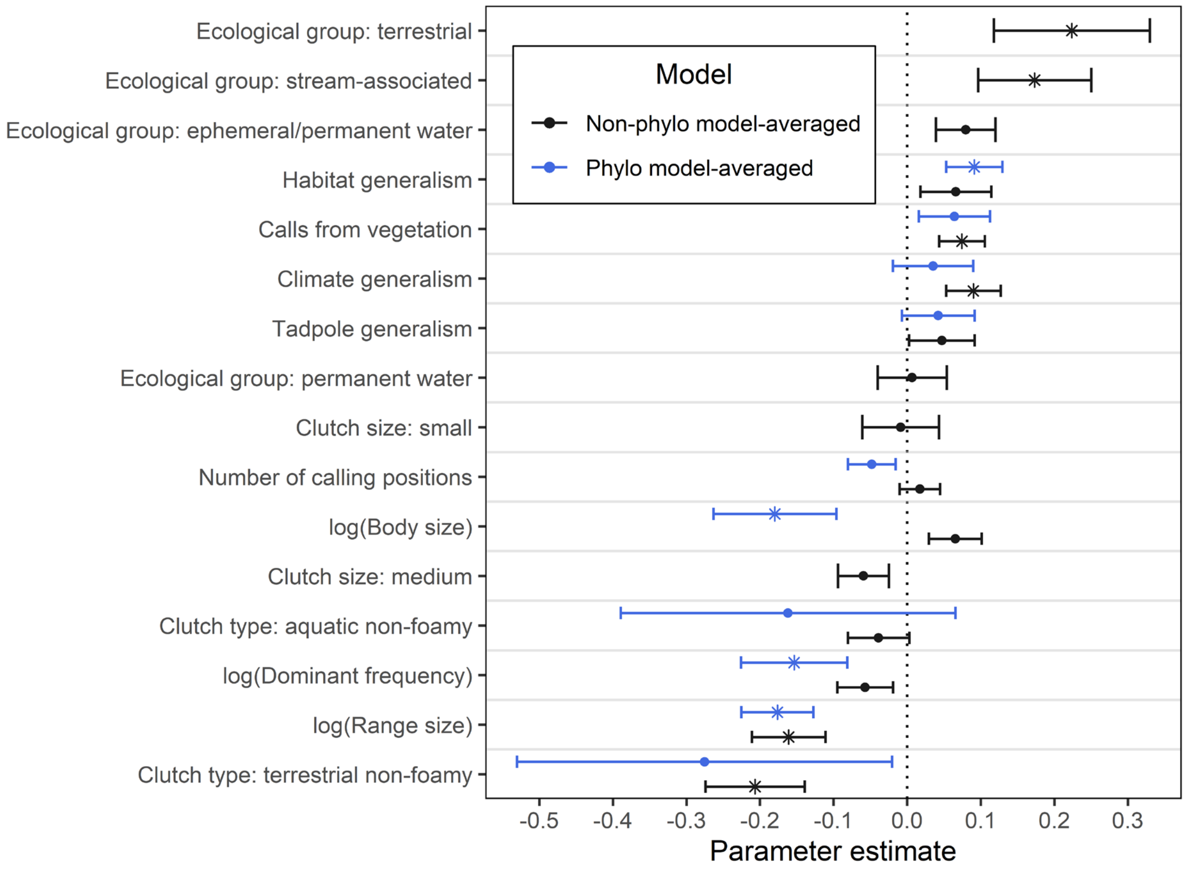
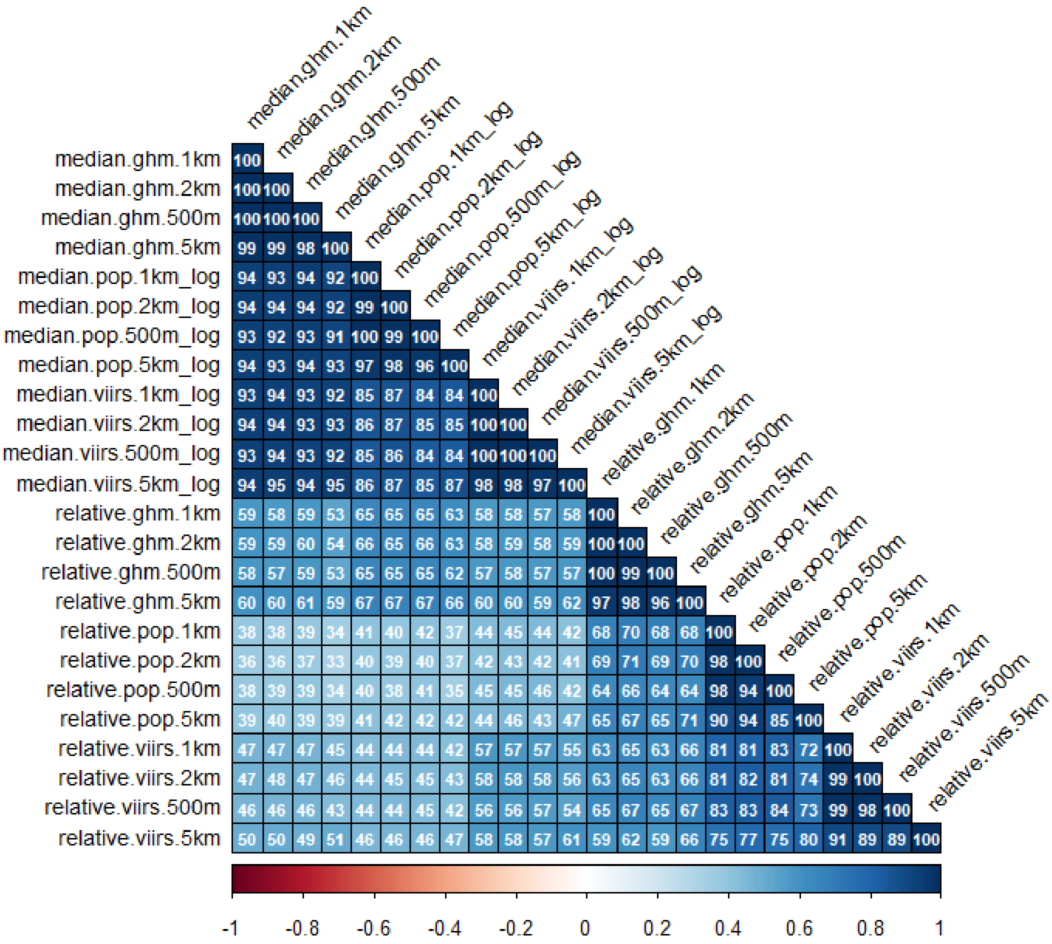


Figure 5. Mean (±SE) standardised parameter estimates for predicted ecological and life history traits for the model-averaged non-phylogenetic and phylogenetically controlled top model sets (* indicate statistically significant traits, p<0.05). Absent traits from the top model set did not have associated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

Supplementary Materials

Quantifying anthropogenic habitat modification

We calculated modification indices using three continuous measures of habitat modification (VIIRS night-time lights; global human modification index, GHM; and UN-adjusted population density) and four buffer sizes (500m, 1km, 2km and 5km). Pixels determined to be water >90% of the time (e.g., oceans) were masked and were therefore excluded from calculations of the indices. The resulting measures of modification were similar regardless of the chosen dataset or buffer size (Figure S1 and Figure S2).



	median.ghm.1km	median.ghm.2km	median.ghm.500m	median.ghm.5km	median.pop.1km_log	median.pop.2km_log	median.pop.500m_log	median.pop.5km_log	median.viirs.1km_log	median.viirs.2km_log	median.viirs.500m_log	median.viirs.5km_log	relative.ghm.1km	relative.ghm.2km	relative.ghm.500m	relative.ghm.5km	relative.pop.1km	relative.pop.2km	relative.pop.500m	relative.pop.5km	relative.viirs.1km	relative.viirs.2km	relative.viirs.500m	relative.viirs.5km
median.ghm.1km	100																							
median.ghm.2km	100	100																						
median.ghm.500m	100	100	100																					
median.ghm.5km	99	99	98	100																				
median.pop.1km_log	94	93	94	92	100																			
median.pop.2km_log	94	94	94	92	99	100																		
median.pop.500m_log	93	92	93	91	100	99	100																	
median.pop.5km_log	94	93	94	93	97	98	96	100																
median.viirs.1km_log	93	94	93	92	85	87	84	84	100															
median.viirs.2km_log	94	94	93	93	86	87	85	85	100	100														
median.viirs.500m_log	93	94	93	92	85	86	84	84	100	100	100													
median.viirs.5km_log	94	95	94	95	86	87	85	87	98	98	97	100												
relative.ghm.1km	59	58	59	53	65	65	65	63	58	58	57	58	100											
relative.ghm.2km	59	59	60	54	66	65	66	63	58	59	58	59	100	100										
relative.ghm.500m	58	57	59	53	65	65	65	62	57	58	57	57	100	99	100									
relative.ghm.5km	60	60	61	59	67	67	67	66	60	60	59	62	97	98	96	100								
relative.pop.1km	38	38	39	34	41	40	42	37	44	45	44	42	68	70	68	68	100							
relative.pop.2km	36	36	37	33	40	39	40	37	42	43	42	41	69	71	69	70	98	100						
relative.pop.500m	38	39	39	34	40	38	41	35	45	45	46	42	64	66	64	64	98	94	100					
relative.pop.5km	39	40	39	39	41	42	42	42	44	46	43	47	65	67	65	71	90	94	85	100				
relative.viirs.1km	47	47	47	45	44	44	44	42	57	57	57	55	63	65	63	66	81	81	83	72	100			
relative.viirs.2km	47	48	47	46	44	45	45	43	58	58	58	56	63	65	63	66	81	82	81	74	99	100		
relative.viirs.500m	46	46	46	43	44	44	45	42	56	56	57	54	65	67	65	67	83	83	84	73	99	98	100	
relative.viirs.5km	50	50	49	51	46	46	46	47	58	58	57	61	59	62	59	66	75	77	75	80	91	89	89	100

Figure S1. Correlation coefficients between three measures of anthropogenic habitat modification, expressed as a percentage. All pairwise comparisons were significant ($P < 0.01$). Modification measures were calculated using three different datasets (global human modification index, GHM; night-time light values, VIIRS; UN-adjusted population density), taking the mean values in a 500m, 1km, 2km or 5km buffer around each georeferenced datapoint. These values were then used to calculate a median score (species' anthropogenic modification score) and relative score (anthropogenic modification index) for each species ($N = 87$). Median scores represented the median anthropogenic modification score of all observations of a species. Species with large median scores were inhabitants of highly modified areas. Relative scores for each species were calculated as the difference between the species' median score and the median modification score of all observations within that species' geographic range. A larger relative score indicated a greater tendency to occur in more modified habitats, compared to other observations within its range.

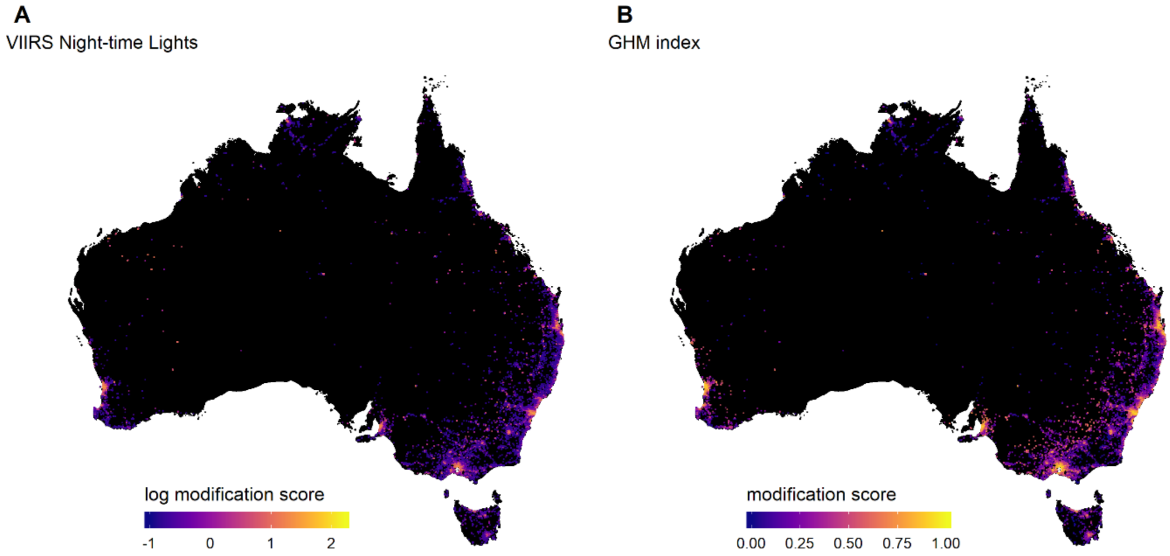


Figure S2. Map comparing two continuous measures of anthropogenic habitat modification across Australia: (A) VIIRS night-time lights (average monthly radiance values, log-transformed) and (B) global human modification (GHM) index. Each coloured point represented an observation submitted to FrogID that was included in analyses.

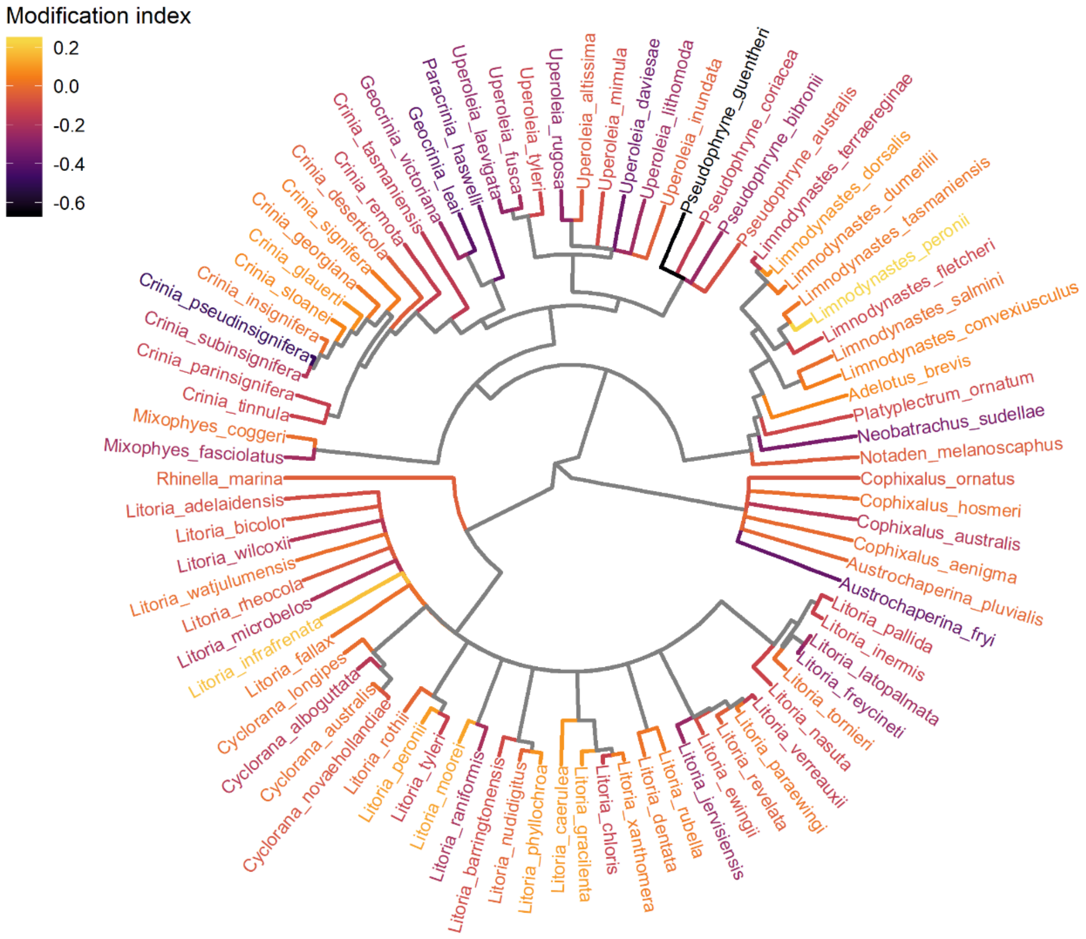


Figure S3. Phylogenetic tree of the 86 species included in our statistical analyses, coloured according to our anthropogenic modification index. A large index (yellow) indicated that the species was tolerant of anthropogenic habitat modification; a small index (dark purple) indicated that the species was intolerant of anthropogenic habitat modification.

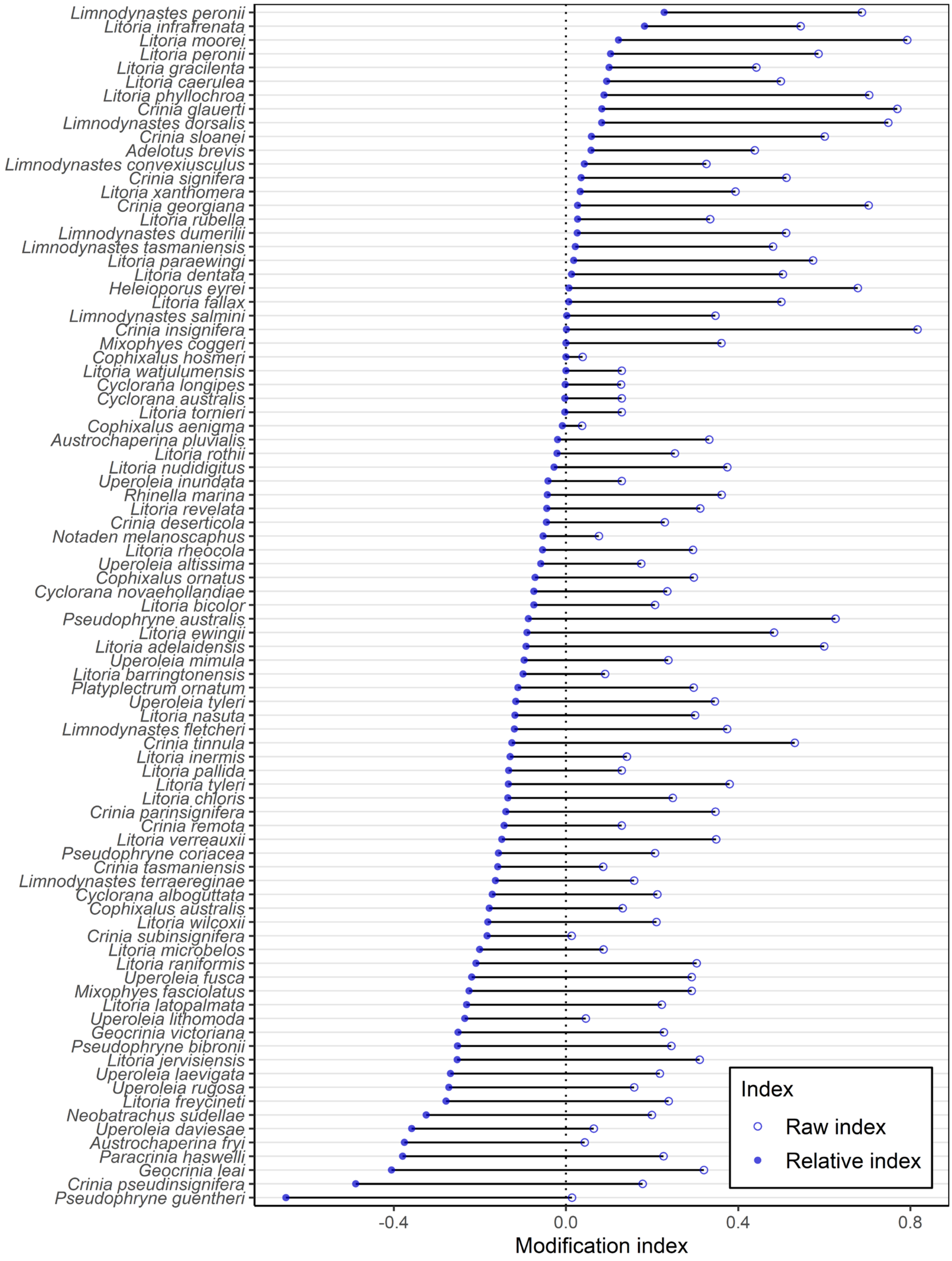


Figure S4. Comparison of the raw (species' anthropogenic modification score) and relative modification indices, calculated from the global human modification (GHM) index, for all 87 species analysed. A relative index of 0 (dotted line) represented no difference between the species' anthropogenic modification score and its geographic range modification score. A positive relative index for any species indicated greater tolerance of anthropogenic habitat modification compared to all observations within the given species' geographic range; a negative index indicated lower tolerance of anthropogenic habitat modification compared to all observations within the given species' geographic range.

Ecological and life history traits

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

Trait	Description and Hypothesis
Life history traits	
Body size[1]	*Description:* Maximum snout-vent length (mm) of males. *Hypothesis:* As large size is associated with slow life history traits (e.g. long lifespan, delayed maturity), larger bodied species may take longer to recover from environmental disturbances than small species and may therefore be less tolerant of habitat modification (Olden, Poff, & Bestgen, 2008; Sodhi et al., 2008). However, size is also positively correlated with dispersal potential, and larger, more mobile species may be advantaged in modified landscapes as they can utilise resources more efficiently across fragmented habitats (Ockinger et al., 2010).
Clutch type[1]	*Description:* 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. *Hypothesis:* Species with terrestrial clutches are often dependent on forest resources (e.g. moist leaf litter) for laying and may not be able to persist in modified habitats where these resources are limited (Nowakowski, Thompson, Donnelly, & Todd, 2017).
Clutch size[1, 2]	*Description:* Typical clutch size, classified broadly into 3 categories: small (<160), medium (160-875) or large (≥876). *Hypothesis:* High fecundity is likely to be favoured in modified environments as it can offset population declines that may result from environmental disturbances and can facilitate quicker colonisation of new habitats (Bielby, Cooper, Cunningham, Garner, & Purvis, 2008; Ockinger et al., 2010).
Adult habitat	
Ecological group[3]	*Description:* Ephemeral pond breeders, E; moist bog/soak associated, M; permanent water associated, P; stream associated, S; or terrestrial breeders, T. *Hypothesis:* Human activities can lead to the creation of new permanent water bodies, such as cattle ponds, which can benefit pond breeding species (Nowakowski, Frishkoff, Thompson, Smith, & Todd, 2018; Valdez et al., 2015). Thus, species associated with permanent water or ponds may be more modification tolerant than stream or terrestrial breeders.

Calls from vegetation[1]	*Description:* Males call from vegetation (yes/no). *Hypothesis:* Species that call from vegetation may be negatively impacted by reductions in canopy cover and vegetation. As vegetation can be less structurally complex in highly modified environments (Le Roux et al., 2014), vegetation dependent species are expected to be less modification tolerant.
Distribution	
Range size	*Description:* Geographic range size (km^2). *Hypothesis:* Small ranges are frequently correlated with low abundance, low reproductive success, and greater habitat specificity. The former two traits can reduce species' resilience to habitat modification, whilst the latter can make it difficult for species to obtain essential resources in fragmented landscapes (Sodhi et al., 2008). Thus, species with larger ranges are expected to be more modification tolerant.
Generalism	
Tadpole generalism[1]	*Description:* Number of positions in the water column occupied by tadpoles (range: 0-3). Possible positions: none, top, middle, bottom. *Hypothesis:* Tadpole positions in the water column are associated with diet and specific morphology (Rossa-Feres, Jim, & Fonseca, 2004). Species that can occupy multiple positions may be better able to exploit a diverse range of resources and, thus, perform better in modified habitats.
Climate generalism	*Description:* Number of climate zones occupied by adult frogs (range: 1-6). There were 6 climates zones: desert, equatorial, grassland, subtropical, temperate, tropical. *Hypothesis:* Generalist species that occupy many climate zones may perform better in modified habitats than species that occupy few climate zones, as they are more likely to be tolerant of a wide range of abiotic conditions (Hirschfeld & Rodel, 2017).
Habitat generalism	*Description:* 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. *Hypothesis:* Generalist species that can tolerate a wide range of habitats are likely to also be tolerant of modified habitats (Hirschfeld & Rodel, 2017).
Number of calling positions[1]	*Description:* Number of calling positions (range: 1-3). Possible positions: above ground; ground/below ground; above water; in water. *Hypothesis:* Species with general microhabitat requirements for calling are more likely to find a suitable calling site in modified habitats and, thus, perform better in these habitats than species with specific microhabitat preferences.
Other	

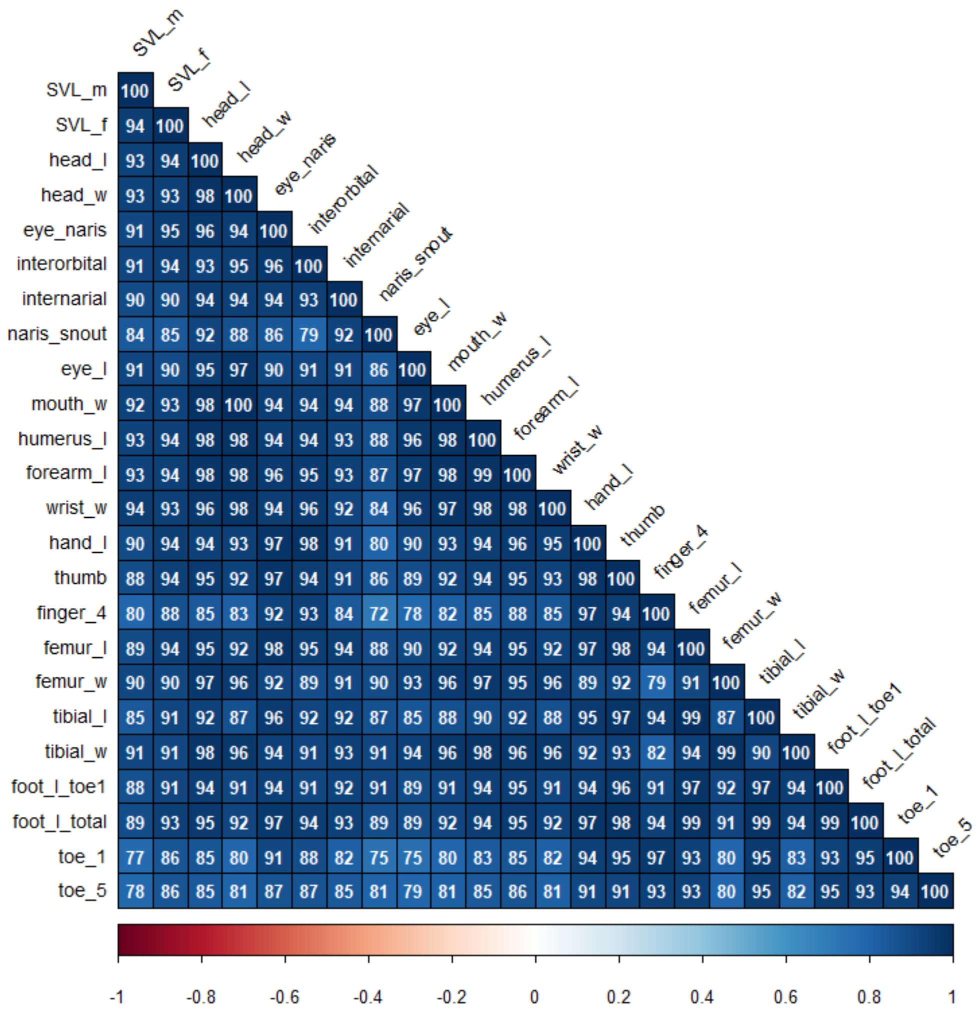
Call dominant frequency[4]	*Description:* Dominant frequency (Hz) of male advertisement calls. We focused on dominant frequency as it is easily quantifiable and less labile (e.g. in response to ambient temperature) than other calling traits (Tonini et al., 2020). *Hypothesis:* Signal transmission can be impeded by excessive noise and physical elements of the calling environment, including vegetation structure (Rabin & Greene, 2002). As low-frequency noise pollution and floristic changes are common in modified landscapes, selection may favour higher call frequencies to facilitate acoustic communication (Roca et al., 2016).

[1] Anstis (2017).

[2] Bielby et al. (2008).

[3] Modified from Murray, Rosauer, McCallum, and Skerratt (2011).

[4] 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).

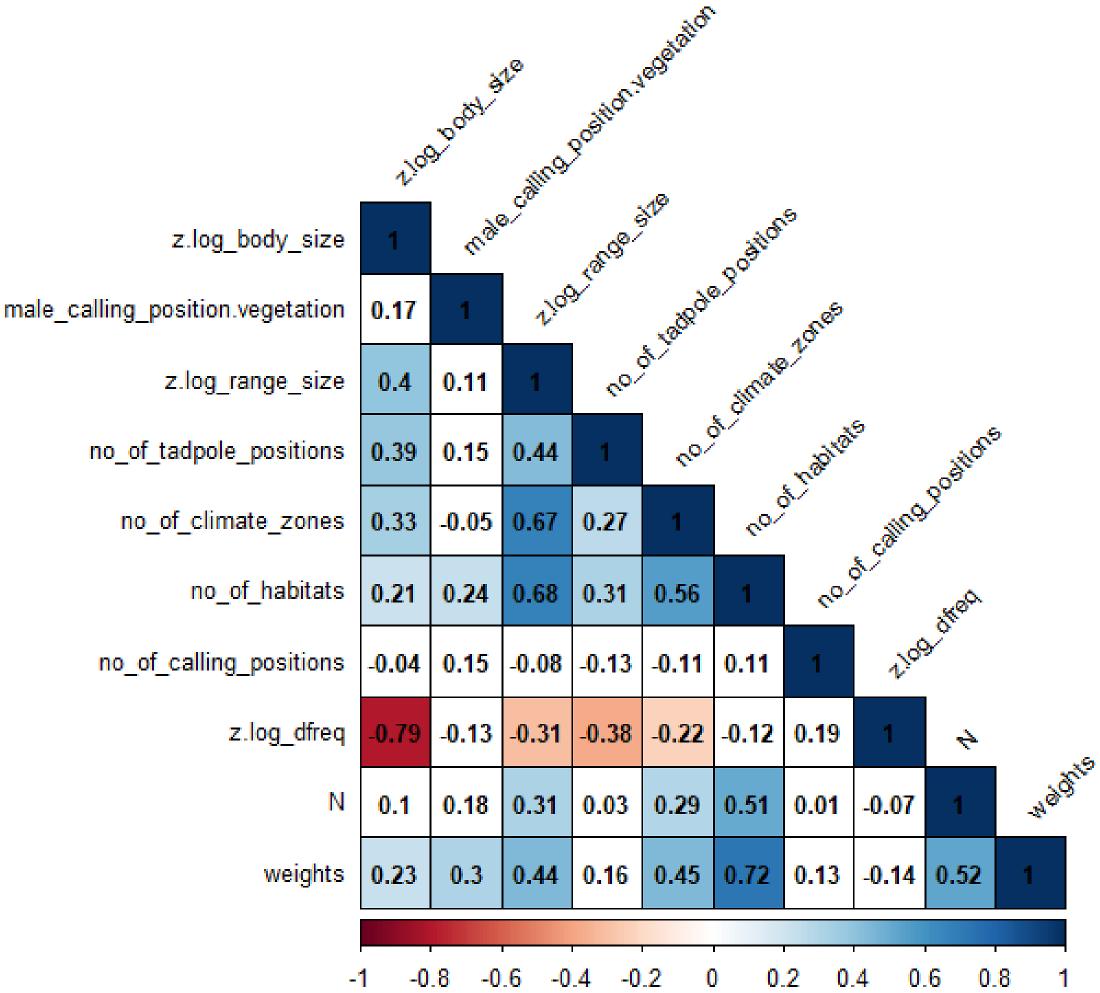


	SVL_m	SVL_f	head_l	head_w	eye_naris	interorbital	internarial	naris_snout	eye_l	mouth_w	humerus_l	forearm_l	wrist_w	hand_l	thumb	finger_4	femur_l	femur_w	tibial_l	tibial_w	foot_l_toe1	foot_l_total	toe_1	toe_5
SVL_m	100																							
SVL_f	94	100																						
head_l	93	94	100																					
head_w	93	93	98	100																				
eye_naris	91	95	96	94	100																			
interorbital	91	94	93	95	96	100																		
internarial	90	90	94	94	94	93	100																	
naris_snout	84	85	92	88	86	79	92	100																
eye_l	91	90	95	97	90	91	91	86	100															
mouth_w	92	93	98	100	94	94	94	88	97	100														
humerus_l	93	94	98	98	94	94	93	88	96	98	100													
forearm_l	93	94	98	98	96	95	93	87	97	98	99	100												
wrist_w	94	93	96	98	94	96	92	84	96	97	98	98	100											
hand_l	90	94	94	93	97	98	91	80	90	93	94	96	95	100										
thumb	88	94	95	92	97	94	91	86	89	92	94	95	93	98	100									
finger_4	80	88	85	83	92	93	84	72	78	82	85	88	85	97	94	100								
femur_l	89	94	95	92	98	95	94	88	90	92	94	95	92	97	98	94	100							
femur_w	90	90	97	96	92	89	91	90	93	96	97	95	96	89	92	79	91	100						
tibial_l	85	91	92	87	96	92	92	87	85	88	90	92	88	95	97	94	99	87	100					
tibial_w	91	91	98	96	94	91	93	91	94	96	98	96	96	92	93	82	94	99	90	100				
foot_l_toe1	88	91	94	91	94	91	92	91	89	91	94	95	91	94	96	91	97	92	97	94	100			
foot_l_total	89	93	95	92	97	94	93	89	89	92	94	95	92	97	98	94	99	91	99	94	99	100		
toe_1	77	86	85	80	91	88	82	75	75	80	83	85	82	94	95	97	93	80	95	83	93	95	100	
toe_5	78	86	85	81	87	87	85	81	79	81	85	86	81	91	91	93	93	80	95	82	95	93	94	100

Figure S5. Correlation coefficients between morphological traits, expressed as a percentage. All pairwise comparisons were significant (*P* < 0.0001). SVL_m = male snout-vent length; SVL_f = female snout-vent length; l = length; w = width.

Table S2. Variance inflation factors for the ecological and life history traits (predictor variables).

Trait	Generalised VIF	Degrees of freedom	Adjusted Generalised VIF
log(Body size)	3.98	1	2.00
Clutch type	4.13	2	1.43
Clutch size category	2.82	2	1.3
Ecological group	5.88	4	1.25
Male calling position: vegetation	1.74	1	1.32
log(Range size)	3.46	1	1.86
Tadpole generalism	2.22	1	1.49
Climate generalism	2.95	1	1.72
Habitat generalism	2.29	1	1.51
Number of calling positions	1.57	1	1.25
log(Dominant frequency)	4.02	1	2.00



	z.log_body_size	male_calling_position.vegetation	z.log_range_size	no_of_tadpole_positions	no_of_climate_zones	no_of_habitats	no_of_calling_positions	z.log_dfreq	N	weights
z.log_body_size	1									
male_calling_position.vegetation	0.17	1								
z.log_range_size	0.4	0.11	1							
no_of_tadpole_positions	0.39	0.15	0.44	1						
no_of_climate_zones	0.33	-0.05	0.67	0.27	1					
no_of_habitats	0.21	0.24	0.68	0.31	0.56	1				
no_of_calling_positions	-0.04	0.15	-0.08	-0.13	-0.11	0.11	1			
z.log_dfreq	-0.79	-0.13	-0.31	-0.38	-0.22	-0.12	0.19	1		
N	0.1	0.18	0.31	0.03	0.29	0.51	0.01	-0.07	1	
weights	0.23	0.3	0.44	0.16	0.45	0.72	0.13	-0.14	0.52	1

Figure S6. Correlation between numerical ecological and life history traits (predictor variables).

Model results

Model-averaged results (non-phylogenetically controlled)

Table S3. Non-phylogenetic top model set (36 models) examining the effect of ecological and life history traits on species' response to anthropogenic habitat modification. Model term codes: 1 = clutch type; 2 = calls from vegetation (yes/no); 3 = climate generalism; 4 = log(body size); 5 = log(range size); 6 = log(dominant frequency); 7 = habitat generalism; 8 = clutch size category; 9 = tadpole generalism; 10 = number of calling positions; 11 = ecological group.

Model terms	df	logLik	AICc	delta	weight
1/2/3/4/5	8	54.43	-90.99	0.00	0.09
1/2/3/5/6	8	54.06	-90.25	0.74	0.06
1/2/3/4/5/7	9	55.28	-90.18	0.80	0.06
1/2/3/5/6/8	10	56.34	-89.75	1.23	0.05
1/2/3/4/5/8	10	56.26	-89.59	1.40	0.05
1/2/3/5/6/7	9	54.92	-89.48	1.51	0.04
1/2/3/4/5/9	9	54.86	-89.36	1.63	0.04
1/2/3/4/5/6	9	54.76	-89.15	1.83	0.04
1/2/3/5/8	9	54.75	-89.13	1.85	0.04
1/2/3/5/6/10	9	54.62	-88.87	2.12	0.03
1/4/5/7/9/11	12	58.54	-88.81	2.18	0.03
1/2/3/5/6/7/8	11	57.16	-88.76	2.23	0.03
1/2/3/4/5/10	9	54.53	-88.69	2.30	0.03
1/2/3/4/5/6/7	10	55.73	-88.53	2.45	0.03
1/2/3/4/5/7/9	10	55.73	-88.53	2.46	0.03
1/2/3/5/8/9	10	55.67	-88.40	2.59	0.03
1/2/3/4/5/7/8	11	56.97	-88.37	2.61	0.02
1/2/3/5/6/9	9	54.22	-88.08	2.91	0.02
1/5/7/8/9/11	13	59.48	-87.91	3.08	0.02
1/2/3/4/5/8/9	11	56.73	-87.90	3.09	0.02
1/2/4/5/7	8	52.83	-87.78	3.21	0.02
1/2/3/5/6/8/10	11	56.67	-87.77	3.22	0.02
1/2/3/5/6/7/10	10	55.33	-87.72	3.27	0.02
1/2/3/4/5/6/8	11	56.63	-87.69	3.30	0.02
1/2/3/4/5/7/10	10	55.30	-87.67	3.32	0.02
1/2/3/5/7/8	10	55.29	-87.65	3.33	0.02
1/2/3/5/6/8/9	11	56.54	-87.52	3.47	0.02
1/4/5/7/8/9/11	14	60.68	-87.45	3.54	0.02
1/2/3/4/5/9/10	10	55.14	-87.35	3.64	0.01
1/2/3/5/6/7/9	10	55.07	-87.20	3.79	0.01

1/3/4/5/7/9/11	13	59.10	-87.15	3.84	0.01
1/2/4/5/7/9/11	13	59.10	-87.14	3.85	0.01
1/2/3/4/5/6/10	10	55.02	-87.12	3.87	0.01
1/3/4/5/7	8	52.47	-87.07	3.92	0.01
1/2/3/4/5/8/10	11	56.31	-87.05	3.94	0.01
1/2/3/4/5/6/9	10	54.98	-87.03	3.95	0.01

Table S4. Non-phylogenetically controlled effect of ecological and life history traits on species' response to anthropogenic modification. Both full average and conditional average summary statistics are presented (estimates; standard error; z scores; p-values, bold for significant). The intercept is the reference level for any categorical traits (e.g., clutch type: aquatic foamy; clutch size: large; ecological group: E; calling position: does not call from vegetation). Ecological group: ephemeral pond breeders, E; permanent water associated, P; ephemeral pond and permanent water associated, E/P; stream associated, S; terrestrial breeders, T.

	Full average					Conditional average				
	Estimate	SE	Adjusted SE	z value	p-value	Estimate	SE	Adjusted SE	z value	p-value
(Intercept)	-0.015	0.044	0.045	0.331	0.741	-0.015	0.044	0.045	0.331	0.741
Clutch type: aquatic non-foamy	-0.039	0.042	0.042	0.922	0.356	-0.039	0.042	0.042	0.922	0.356
Clutch type: terrestrial non-foamy	-0.207	0.067	0.068	3.019	**0.003**	-0.207	0.067	0.068	3.019	**0.003**
Calls from vegetation	0.067	0.037	0.037	1.830	0.067	0.074	0.031	0.031	2.368	**0.018**
Climate generalism	0.081	0.044	0.045	1.814	0.070	0.090	0.037	0.038	2.384	**0.017**
log(Body size)	0.039	0.042	0.043	0.915	0.360	0.065	0.036	0.036	1.798	0.072
log(Range size)	-0.161	0.050	0.051	3.177	**0.001**	-0.161	0.050	0.051	3.177	**0.001**
log(Dominant frequency)	-0.024	0.037	0.037	0.630	0.529	-0.057	0.038	0.038	1.487	0.137
Habitat generalism	0.027	0.045	0.045	0.595	0.552	0.066	0.048	0.049	1.355	0.175
Clutch size: medium	-0.021	0.035	0.035	0.590	0.555	-0.059	0.035	0.035	1.689	0.091
Clutch size: small	-0.003	0.031	0.032	0.099	0.921	-0.009	0.052	0.053	0.169	0.866
Tadpole generalism	0.013	0.032	0.032	0.418	0.676	0.047	0.045	0.045	1.049	0.294
Number of calling positions	0.003	0.012	0.013	0.211	0.833	0.017	0.027	0.028	0.616	0.538
Ecological group: E/P	0.007	0.026	0.026	0.281	0.779	0.079	0.040	0.041	1.931	0.053
Ecological group: P	0.001	0.015	0.015	0.043	0.966	0.007	0.047	0.048	0.141	0.888
Ecological group: S	0.016	0.055	0.056	0.289	0.772	0.173	0.077	0.078	2.216	**0.027**
Ecological group: T	0.021	0.073	0.073	0.286	0.775	0.224	0.106	0.108	2.078	**0.038**

'Best' model (non-phylogenetically controlled)

Table S5. The top non-phylogenetic model (lowest AICc) of the effect of ecological and life history traits on species' response to anthropogenic habitat modification.

	Estimate	SE	t value	p-value
(Intercept)	-0.015	0.035	-0.417	0.678
Clutch type: aquatic non-foamy	-0.041	0.036	-1.130	0.262
Clutch type: terrestrial non-foamy	-0.207	0.064	-3.247	**0.002**
Calls from vegetation	0.079	0.029	2.697	**0.009**
Climate generalism	0.092	0.035	2.632	**0.010**
log(Body size)	0.073	0.028	2.592	**0.011**
log(Range size)	-0.156	0.048	-3.264	**0.002**

Weighted Residuals

Min	1Q	Median	3Q	Max
-8.945	-1.807	-0.059	1.358	7.181

Residual standard error: 2.801 on 79 degrees of freedom
Multiple R-squared: 0.3541, Adjusted R-squared: 0.3051
F-statistic: 7.219 on 6 and 79 DF, p-value: 3.656e-06

Model-averaged results (phylogenetically controlled)

Table S6. Phylogenetic top model set (30 models) examining the effect of ecological and life history traits on species' response to anthropogenic habitat modification. Term codes: 1 = number of calling positions; 2 = habitat generalism; 3 = log(body size); 4 = log(dominant frequency); 5 = log(range size); 6 = calls from vegetation (yes/no); 7 = tadpole generalism; 8 = climate generalism; 9 = clutch type.

Model terms	df	logLik	AICc	delta	weight
1/2/3/4/5	7	22.60	-29.76	0.00	0.11
2/3/4/5	6	21.36	-29.66	0.11	0.11
1/2/3/4/5/6	8	23.36	-28.85	0.91	0.07
2/3/4/5/6	7	22.07	-28.71	1.06	0.07
2/3/4/5/7	7	21.72	-28.01	1.75	0.05
1/2/3/4/5/7	8	22.89	-27.92	1.84	0.04
2/3/4/5/8	7	21.57	-27.70	2.06	0.04
2/5/6	5	19.04	-27.33	2.43	0.03
1/2/3/4/5/8	8	22.60	-27.33	2.43	0.03
1/2/4/5/6	7	21.25	-27.07	2.69	0.03
1/2/5/6	6	20.06	-27.05	2.71	0.03
2/3/4/5/6/8	8	22.45	-27.04	2.73	0.03
1/2/4/5	6	19.88	-26.70	3.06	0.02
2/3/4/5/6/7	8	22.28	-26.68	3.08	0.02
2/4/5/6	6	19.86	-26.66	3.10	0.02
1/2/3/4/5/6/7	9	23.51	-26.65	3.11	0.02
2/5	4	17.53	-26.56	3.20	0.02
1/2/3/4/5/6/8	9	23.39	-26.41	3.35	0.02
2/5/7	5	18.57	-26.39	3.38	0.02
2/4/5	5	18.55	-26.34	3.42	0.02
1/2/3/4/5/9	9	23.34	-26.32	3.44	0.02
2/5/6/7	6	19.64	-26.22	3.55	0.02
3/4/5/8	6	19.62	-26.18	3.59	0.02
1/2/5	5	18.46	-26.16	3.60	0.02
3/4/5/6/8	7	20.77	-26.10	3.67	0.02
2/3/4/5/9	8	21.95	-26.03	3.73	0.02
1/2/5/7	6	19.51	-25.96	3.80	0.02
2/3/4/5/7/8	8	21.91	-25.94	3.82	0.02
2/5/6/8	6	19.49	-25.91	3.85	0.02
1/2/5/6/7	7	20.65	-25.87	3.89	0.02

Table S7. Phylogenetically controlled effect of ecological and life history traits on species' response to anthropogenic modification. Both full average and conditional average summary statistics are presented (estimates; standard error; z scores; p-values, bold for significant). The intercept is the reference level for any categorical traits (e.g., clutch type: aquatic foamy; calling position: does not call from vegetation).

	Full average				Conditional average			
	Estimate	SE	z value	p-value	Estimate	SE	z value	p-value
(Intercept)	-0.108	0.209	0.516	0.606	-0.108	0.209	0.516	0.606
Number of calling positions	-0.022	0.033	0.681	0.496	-0.048	0.032	1.484	0.138
Habitat generalism	0.088	0.041	2.124	**0.034**	0.091	0.038	2.378	**0.017**
log(Body size)	-0.128	0.108	1.185	0.236	-0.180	0.083	2.156	**0.031**
log(Dominant frequency)	-0.124	0.089	1.396	0.163	-0.154	0.072	2.124	**0.034**
log(Range size)	-0.176	0.049	3.597	**<0.001**	-0.176	0.049	3.597	**<0.001**
Calls from vegetation	0.027	0.045	0.604	0.546	0.064	0.049	1.324	0.186
Tadpole generalism	0.010	0.030	0.326	0.744	0.042	0.050	0.851	0.395
Climate generalism	0.007	0.028	0.245	0.807	0.035	0.055	0.644	0.520
Clutch type: aquatic non-foamy	-0.006	0.054	0.113	0.910	-0.162	0.227	0.712	0.476
Clutch type: terrestrial non-foamy	-0.010	0.072	0.144	0.886	-0.275	0.255	1.081	0.280

'Best' model (phylogenetically controlled)

Table S8. The top phylogenetic model (lowest AICc) of the effect of ecological and life history traits on species' response to anthropogenic habitat modification.

	Estimate	SE	t value	p-value
(Intercept)	-0.127	0.199	-0.639	0.525
Number of calling positions	-0.049	0.032	-1.530	0.130
Habitat generalism	0.092	0.036	2.527	**0.013**
log(Body size)	-0.186	0.082	-2.285	**0.025**
log(Dominant frequency)	-0.179	0.066	-2.725	**0.008**
log(Range size)	-0.183	0.047	-3.852	**<0.001**

AIC	logLik
-31.2	22.6

Raw residuals

Min	1Q	Median	3Q	Max
-0.53886	-0.07059	0.05061	0.14709	0.45502

Mean tip height: 170.7992
sigma2: 0.0009946398

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