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Received: 15 November 2021 | Accepted: 2 June 2022

DOI: 10.1111/1365-2435.14140

Functional Ecology | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Animal Functional Traits

Using functional traits to identify conservation priorities for the world's crocodylians

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Handling Editor: Joseph Tobias

Abstract

1. Over half of all crocodylians are threatened with extinction, with many species considered to be functionally extinct throughout their historical ranges. How such losses impact crocodylian functional diversity (FD) and its conservation is poorly understood, but can be investigated using measurable traits. Where such information is unavailable, phylogenetic diversity (PD) has been proposed as an effective strategy to capture FD, but this assumption is not well tested.
2. We constructed a global trait database for 28 extant crocodylians, and quantified their FD, distinctiveness and groupings. Functionally distinctive crocodylians include the most and least evolutionarily distinct species, likely because unusual trait values and combinations can be produced by both evolutionary isolation and evolutionarily recent adaptive radiation. We identified four functional groups of crocodylians, within which species have similar ecological roles. Highly distinctive species, such as the gharial, fit less well into functional groups.
3. We combined functional distinctiveness (FUD) and threat ranking scores to prioritise species for conservation. The metric is termed Ecologically Distinct and Globally Endangered (EcoDGE), and we tested how well it operates to preserve crocodylian FD among extant Crocodylia. Under current extinction scenarios, 32%–38% of crocodylian FD might be lost within 100 years. Losses increase to 48% if all threatened species go extinct, with Asia identified as a hotspot of threatened FD in crocodylians. Highly threatened distinctive species lead this extinction scenario, exacerbated by clusters of species sharing traits linked to high extinction risk. These traits include habitat specialism and lower reproductive investment; in contrast, species that tolerate climate extremes are more resilient.
4. Prioritising at-risk species based on FUD and threat status appears to be an effective way to conserve present-day crocodylian diversity. Conservation prioritisation based on the EcoDGE metric performed well to minimise projected losses in FD. Among extant crocodylians, FD losses are projected when high diversity overlaps with high extrinsic threats.
5. We then examined the utility of PD-based measures as surrogates for FD conservation, to better understand the advantages and drawbacks of such substitutions.

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A PD-based measure such as the Evolutionarily Distinct and Globally Endangered metric provided an effective tool to capture FD in our tests.

KEYWORDS
conservation prioritisation, Crocodylia, EDGE, extinction risk, functional distinctiveness, functional diversity

1 | INTRODUCTION

Human impacts on global ecosystems have led to major losses of species worldwide (Dirzo et al., 2014; Hull et al., 2015). As species become increasingly rare and decline towards extinction, they cease to perform functional roles in their ecosystems, which has the potential to cause cascading ecological impacts (Valiente-Banuet et al., 2014). Indeed, species often become functionally extinct in most of their range long before final extinction (McConkey & O'Farrill, 2015; Valiente-Banuet et al., 2014). Conservation of the global pool of biodiversity is vitally important, and should consider all facets of biodiversity, including functional diversity (FD; Pollock et al., 2020).

The functional role of a species can be estimated through an assemblage of functional traits, that is, traits which impact fitness via their effects on growth, reproduction and survival (Violle et al., 2007). Traits can be used to determine FD in a taxonomic group (e.g. Pollock et al., 2017) or in an ecological community (e.g. Murgier et al., 2021). Functionally distinctive species are those which have unusual or unique trait values and/or trait combinations (Dee et al., 2019), and are therefore likely to be ecologically irreplaceable (Violle et al., 2017). Irreplaceability and vulnerability are key concepts for prioritisation in biodiversity conservation (Brooks et al., 2006), and prioritising conservation of multiple components of global biodiversity is also important for maintaining future options for natural systems to support human society (IPBES, 2019).

Understanding the functional roles of species in their ecosystem can inform ecological studies and conservation planning. However, populations of many species are now so depleted that field studies in most or all sites of former occurrence are often impossible. Transferring knowledge from one species to others is therefore of increasing importance, and can be informed by patterns of FD within a taxonomic group, such as functional groupings (Blaum et al., 2011); species with similar sets of traits may respond similarly to environmental change or to conservation interventions, whereas functionally distinctive species are likely to have a more idiosyncratic response.

Measures of diversity other than a direct metric of FD can also be employed in conservation prioritisation (Petchey & Gaston, 2006). For freshwater species, large population declines and limited extinction risk data (He et al., 2018), coupled with difficulties of obtaining functional trait data (Schmera et al., 2017), necessitate alternative measures. One such metric is phylogenetic diversity (PD), which captures the unique evolutionary history of a set of species (Faith, 1992). PD may also play a dual role as a useful surrogate for capturing FD (Redding & Mooers, 2015; Tucker et al., 2019). PD-based estimates measure feature diversity (not just function) across the tree of life, with the aim to conserve current and future unknown benefits that biodiversity can provide (Molina-Venegas et al., 2021). PD has been integrated directly into practical conservation priority setting through the Evolutionarily Distinct and Globally Endangered (EDGE) metric, which ranks species based on their Evolutionary Distinctiveness (ED) and IUCN Red List status (Isaac et al., 2007).

Crocodylia is an order comprised of just ~28 extant species exhibiting a broadly similar within-order biology, distinct from that of other extant vertebrates (Colston et al., 2020; Uetz, 2022). This unusual biology means that crocodylians are functionally unique within their freshwater ecosystems and, as ectotherms, can reach higher densities than equivalently sized endothermic apex predators. This suggests that crocodylians play important and irreplaceable ecological roles (Somaweera et al., 2020). As a first step to understanding the identity and diversity of these roles, functional similarities and differences across crocodylian species could be determined using traits specifically selected to capture the distinct ecological functions of the group.

Traits can also be used as a quantitative metric to identify conservation priorities for threatened FD (e.g. Hidasi-Neto et al., 2015), and therefore to inform decisions on how to conserve this diversity as a key facet of global crocodylian biodiversity. This need is urgent as over half of the assessed crocodylian species are threatened, with several Critically Endangered species already extirpated or functionally extinct across most of their ranges (IUCN, 2021). A trait-based approach can also be used to understand the mechanisms of extinction risk (Cardillo et al., 2008). Traits that correlate with extinction vulnerability include low rates of reproduction (Pincheira-Donoso et al., 2021; Purvis et al., 2000) and habitat specialisation (Böhm et al., 2016 Isaac, 2009), and if such traits are found in functionally distinctive species and/or in groups of functionally similar species, the loss of FD will be accelerated as such species go extinct. Taken together, these considerations indicate that a functional approach should improve conservation planning for crocodylians.

The highly derived biology of crocodylians means that a narrow taxonomic approach is likely to be more precise for both comparative models and functional comparison (Cardillo et al., 2008); in multi-taxa analyses investigating extinction risk, the signal of the species-poor order of crocodylians is swamped (e.g. Colston et al., 2020). Additionally, broad functional traits (e.g. 'terrestrial/aquatic') could mask subtler functionally important differences which are relevant for understanding differing susceptibilities to similar threats. For example, in South Asia, the gharial *Gavialis gangeticus*, a highly aquatic specialist with limited terrestrial capabilities, is Critically

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Endangered, but the sympatric mugger crocodile *Crocodylus palustris*, a habitat generalist that moves considerable overland distances, is merely Vulnerable (IUCN, 2021).

Using crocodylians as a case study, we constructed a novel database of specific functional traits of extant species. Using simulations of extinctions on functional trait dendrograms, we predict losses of FD, and how patterns of functional distinctiveness (FUD) and clustering may lead to these projected losses. We investigate the associations between extinction risk and traits, to determine which intrinsic traits influence susceptibility to threats. Using a metric that combines FUD and extinction risk data [Ecologically Distinct and Globally Endangered (EcoDGE); Hidasi-Neto et al., 2015], we determine whether prioritisation of species with this metric is effective for conserving FD. We compare this metric with other prioritisation schemes, in particular the EDGE metric as a stand-in estimator for imperilled FD when comprehensive trait information is lacking. Our results not only suggest useful functional groupings and patterns within crocodylians, but also provide wider insights into the value of using various diversity estimators to understand and prioritise conservation actions.

2 | MATERIALS AND METHODS

2.1 | Crocodylian phylogeny

For this analysis, we included 28 crocodylian species (Supporting Information, Methods). For phylogenetic analyses, we used the dated phylogenies from Colston et al. (2020) (Figure 2), which contain 27 of the species in our dataset and provided a distribution of phylogenetic hypotheses, allowing us to incorporate phylogenetic uncertainty. The 28th species, the recently described Hall's New Guinea crocodile *Crocodylus halli*, was excluded from analyses requiring phylogenetic information. For extinction risk analyses, we used the maximum-likelihood tree, which is suitable as this phylogeny does not use taxonomic imputation (Rabosky, 2015). For all other analyses, we used 100 unique trees randomly selected from the posterior distribution of 10,000 dated phylogenies in Colston et al. (2020).

2.2 | Traits database

We compiled a database of 12 traits considered to be functionally relevant from the published literature, grey literature and personal communications with experts (Griffith et al., 2022). These are traits related to diet/foraging strategy (skull shape, bite force), reproduction [nest type, relative clutch mass (RCM)], body size (largest male size, female size at maturity), habitat type (generality, salt tolerance, terrestriality), tolerance of extreme climates (aestivation, brumation) and potential to act as ecosystem engineers (ability to dig burrows). Many traits will have impacts across functional categories (e.g. terrestriality will influence diet and foraging strategy, as well as habitat type and factors such as dispersal ability).

2.3 | Statistical analysis

2.3.1 | Construction of functional trait dendrograms

We carried out all statistical analyses in R version 4.0.5 (R Core Team, 2021). We constructed functional trait dendrograms to investigate functional groups and diversity, following Pollock et al. (2017). We calculated pairwise species dissimilarity with a generalised Gower's distance matrix, which accommodates continuous, ordinal and binary variables. We then generated a dendrogram for all species including all traits, using an unweighted pair group arithmetic mean hierarchical clustering method. We repeated the dendrogram construction, dropping random combinations of 1–3 traits from the analysis each time to capture uncertainty and reduce the impact of specific traits on the results. We repeated this process to generate a distribution of 100 trees. Dendrograms produce similarity hierarchies comparable to phylogenetic trees, enabling us to use analogous techniques for investigating functional and PD in our analyses.

2.3.2 | Calculating functional and evolutionary distinctiveness

To estimate the contribution of each individual species to crocodylian FD, we calculated 'FUD' using the fair proportion metric (Redding, 2003). This metric determines the contribution of each individual taxon to a tree (i.e. functional dendrogram tree) by apportioning the length of each branch equally between all species tips of that branch (Redding, 2003). We calculated the FUD for each tree in the distributions of 100 unique trees, and took the median value for each species as the representative FUD score. We then repeated this method using phylogenetic trees to obtain an 'ED' score to estimate the contribution of each species to crocodylian PD. We used the fair proportion metric for both distinctiveness measures as it is used to calculate ED, which is the most widely used measure of evolutionary uniqueness (Faith et al., 2018) and for comparable scores of FUD (Hidasi-Neto et al., 2015).

The EcoDGE metric is derived from the EDGE metric, and combines the FUD of a species with a measure of threat based upon Red List status, to rank species for conservation priority with the aim of conserving FD (Hidasi-Neto et al., 2015). We calculated EcoDGE scores for each crocodylian species, multiplying our FUD scores by 100 to balance the weighting of the two component values of the EcoDGE metric:

$$\text{EcoDGE} = \ln(1 + \text{FUD}) + \text{GE}^{*} \ln(2),$$

where GE is the Red List category weight [Least Concern (LC) = 0, Near Threatened (NT) = 1, Vulnerable (VU) = 2, Endangered (EN) = 3, Critically Endangered (CR) = 4 (Purvis et al., 2000)].

We also calculated the EDGE score for each crocodylian species to provide an updated EDGE score for each species and scores for new species, based on the Colston et al. (2020) phylogeny. For

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recently split species, we contacted Red List evaluators to request the probable Red List status from draft evaluations.

2.3.3 | Relationship between functional and evolutionary distinctiveness

To determine the relationship between ED and FUD scores, we ran two regression models. We transformed ED and FUD to achieve normality, and after visual inspection used a quadratic and a piecewise regression approach (using the R package SEGMENTED, in which a single breakpoint in the model is estimated used a maximum likelihood approach; Muggeo, 2008), and selected the model which best fit the data. To examine the relationship between FUD or ED and extinction risk, we conducted generalised linear models where Red List status (categorised as 0–4) was regressed against FUD or ED as the predictor variable, and where a binary measure of CR/not CR was regressed against the same predictor variables, since high probabilities of extinction of CR species drive extinction scenarios.

2.3.4 | Correlates of extinction risk

To assess traits correlated with extinction risk, we used Red List categories as response variables and all traits from our database as explanatory variables in a phylogenetic generalised linear model (pGLS), which controls for shared ancestry (Böhm et al., 2016) and is appropriate for our ordinal, continuous and binary trait data (Symonds & Blomberg, 2014). RCM, male and female size, and skull measures were log-transformed to achieve normality. As in the previous analyses, extinction risk was quantified using Red List status categorised as 0–4. Not evaluated species were treated as in (b). We implemented analyses in the R package CAPER (Orme et al., 2013). We first ran univariate pGLS of all predictors on extinction risk, and then carried out stepwise multiple regressions to produce minimum adequate models (MAMs) to explain extinction risk, following Purvis et al. (2000). To reduce the possibility of Type 1 errors due to testing multiple hypotheses on non-independent data subsets, we used Bonferroni corrections of *p*-values during stepwise regression (Böhm et al., 2016).

2.3.5 | Extinction projections

To estimate the percentage of functional and PD of crocodylians likely to be lost under current levels of threat, we simulated extinction scenarios using probabilities of extinction *p*(ext). We randomly selected a tree from the existing distribution of 100 trees (either functional dendrograms or phylogenetic trees) and ran a scenario where each species had a probability *p*(ext) of going extinct, and determined the change in FD or PD in the tree before and after extinctions (Faith, 2008). We repeated this process 1,000 times for both sets, and determined the median change.

For *p*(ext) we followed Davis et al. (2018), who extrapolated this value from Red List criterion E; for CR species, *p*(ext) = 0.999, EN = 0.6723, VU = 0.1, NT = 0.0141 and LC = 0.0017. As these are extrapolations of 'minimum risk of extinction' to qualify for each threat category, and the within-category range could be substantial (e.g. a VU species could be close to either NT or EN), we also ran a 'pessimistic' scenario in which EN species were assigned *p*(ext) = 0.8991, VU = 0.605, NT = 0.09 and LC = 0.01269 (i.e. up to within 10% of the classification of the higher threat category). We also ran a scenario that assumed all threatened species would go extinct.

To determine if more functional and PD was currently threatened than if extinction risk was randomly distributed across the functional and phylogenetic trees of crocodylians, we created a null comparison in which we randomly assigned species to threat categories, but retained the same total number of species in each category. We then repeated the same process as above. We calculated effect size using Hedges' *g* (Hedges, 1981). A large effect size means more diversity is lost than if extinction risk is distributed at random, suggesting threatened species are clustered and/or highly distinctive.

2.3.6 | Gain of FD under different conservation schemes

We investigated the gain in FD under different currently used conservation prioritisation schemes, by sequentially protecting 1–16 species (16 = all threatened species) under the following methods:

1. EcoDGE ranking
2. EDGE ranking
3. Red List status, from most to least threatened (with random sampling within category)
4. Random draw from the 16 threatened species, to create a conservative null model (after Redding & Mooers, 2015)

For each method, we ran the extinction scenario 100 times for each number of species protected (i.e. 1,500 total runs per prioritisation measure) and calculated the median change in FD per species protected. We repeated this for each prioritisation measure, and compared the accumulation curves at the 25%, 50% and 75% quartiles. The use of the 'optimistic' and 'pessimistic' extinction scenarios from (d) gave similar results when comparing between methods, so we report only the 'optimistic' scenario.

3 | RESULTS

3.1 | Functional and Evolutionary Distinctiveness, EcoDGE and EDGE

The gharial is the most functionally distinct crocodylian (Figure 1), with a score 100% more distinct than the next species, and the highest distinctiveness score in all functional dendrograms. Since the

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FIGURE 1 Clockwise from top left: *Gavialis gangeticus* skull and male and female; *Crocodylus porosus* skull and individual in ocean; *Alligator sinensis* skull and male and female; *Osteolaemus afzelli* skull and adult; *Tomistoma schlegelii* skull and adult; and *Mecistops cataphractus* skull and adult, showing convergent evolution with *Tomistoma*.

gharial was so distinct, we repeated all analyses with the gharial excluded; although this impacted some effect sizes, it did not alter any overall conclusions, so we retained gharial in final analyses. The gharial also ranked highest for conservation prioritisation based on EcoDGE scores, followed by the Chinese alligator *Alligator sinensis* and Orinoco crocodile *Crocodylus intermedius*. ED and EDGE scores calculated in this study (Table 1) had similar scores and rankings to previous studies on ED and EDGE in reptiles (Gumbs et al., 2018).

3.2 | Functional groupings

The clustering of species within the functional dendrograms showed four functional groupings (Figure 2, groupings A, B, C and D). Grouping A are fecund species with short, broad skulls, which are tolerant of environmental extremes but mostly lack physiological tolerance of saltwater. Grouping B are fairly terrestrial species, which are known to hunt on land and spend periods of time away from the water. Grouping C are 'classic crocodiles', mostly extreme habitat and dietary generalists that will take terrestrial prey at the water's edge, and are physiologically tolerant of saltwater. Grouping D are highly aquatic, mostly freshwater species that predominantly consume aquatic prey. Groupings A and B appeared to be the most similar, being unresolved in 39% of trees (Supporting Information, Results).

3.3 | Relationship between functional and evolutionary distinctiveness

A linear function with a breakpoint just above the median ED value (Figure 3) best describes the relationship between ED and FUD, accounting for 30% of variation ($T = -2.097/2.845$, $df = 23$, $p < 0.05$). This suggests the most functionally distinctive crocodylian species are those with the highest and lowest ED. The GLM for ED did not find a significant relationship between Red List category and either FUD or ED of crocodylians. The GLM for CR/not CR against FUD found a positive relationship that is nearly significant at $\alpha = 0.05$, with functionally distinctive species more likely to be CR (estimate = 2.9, $df = 26$, $p = 0.09$); limited significance could be due to our small sample size ($n = 27$).

3.4 | Correlates of extinction risk

The MAM accounted for 56% of total variance (Table 2), suggesting that species have a greater threat of extinction if they are habitat specialists and have a lower RCM. Models with additional covariates had significant multicollinearity, with habitat generality being positively correlated with burrowing ability, and with ability to aestivate being positively correlated with burrowing ability.

Several other variables were also significantly correlated with extinction risk in univariate pGLS (Table 3). Species are more at risk if they do not dig burrows, are not known to aestivate, are habitat specialists and have a lower RCM.

3.5 | Extinction projections

Our models project that 32%–38% of crocodylian FD is likely to be lost within 100 years, compared to an estimate of 20%–30% if threat status was randomly distributed among species. This increases to 48% of FD if all threatened species were to go extinct (Figure 4; Table S4), compared to 41% if threat was allocated randomly. Our models also project that 19%–31% of

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TABLE 1 Functional distinctiveness (FUD), evolutionary distinctiveness (ED), Ecologically Distinct and Globally Endangered (EcoDGE) and Evolutionarily Distinct and Globally Endangered (EDGE) scores and IUCN Red List categories for all 28 crocodylian species, ordered from most to least functionally distinct.

Species	Species code	FUD	ED	EcoDGE	EDGE	IUCN
Gavialis gangeticus	GG	23.55	41.26	5.97	6.52	CR
Crocodylus porosus	CPo	10.73	14.78	2.46	2.76	LC
Caiman latirostris	CaL	10.57	25.99	2.45	3.3	LC
Alligator mississippiensis	AM	9.18	47.42	2.32	3.88	LC
Alligator sinensis	AS	9.13	47.42	5.09	6.65	CR
Crocodylus johnsoni	CJ	8.92	19.65	2.29	3.03	LC
Crocodylus intermedius	CI	8.76	11.52	5.05	5.3	CR
Crocodylus rhombifer	CR	8.38	13.3	5.01	5.43	CR
Crocodylus mindorensis	CMi	8.02	16.4	4.97	5.63	CR
Crocodylus siamensis	CSi	7.85	14.78	4.95	5.53	CR
Crocodylus acutus	CA	7.43	11.52	3.52	3.91	VU
Crocodylus niloticus	CNi	7.29	15.68	2.12	2.81	LC
Melanosuchus niger	MN	7.22	29.26	2.80	4.1	NT
Crocodylus moreletii	CMo	7.11	13.3	2.09	2.66	LC
Crocodylus palustris	CPa	6.55	19.1	3.41	4.39	VU
Crocodylus suchus	CS	6.52	17.98	3.40	4.33	VU
Caiman crocodilus	CaC	6.20	21.95	1.97	3.13	LC
Caiman yacare	CaY	6.16	21.95	1.97	3.13	LC
Tomistoma schlegelii	TS	6.04	41.26	3.34	5.13	VU
Paleosuchus trigonatus	PT	5.74	33.66	1.91	3.55	LC
Paleosuchus palpebrosus	PP	5.68	33.66	1.90	3.55	LC
Crocodylus novaeguineae	CNo	5.24	16.4	1.83	2.86	LC
Crocodylus halli	CH	5.20		1.83		LC
Osteolaemus osborni	OO	4.98	22.79	3.18	4.56	VU
Osteolaemus afzelli	OA	4.78	20.4	3.83	4.45	EN
Osteolaemus tetraspis	OT	4.72	20.4	3.13	4.45	VU
Mecistops cataphractus	MC	4.62	22.51	4.50	5.93	CR
Mecistops leptorhynchus	ML	4.62	22.51	3.81	5.93	EN

Abbreviations: CR, critically endangered; EN, endangered; LC, least concern; NT, near threatened; VU, vulnerable.

crocodylian PD is likely to be lost within 100 years, compared to an estimate of 17%–26% if threat status was randomly distributed among species (Figure 4; Table S5). This represents the loss of 115–191 MY of PD, or a loss of 271 MY of PD and 44% of PD if all threatened species went extinct, compared to 35% if threat was allocated randomly.

3.6 | Gain of FD under different conservation schemes

FD was recovered most quickly and consistently by prioritisation using the EcoDGE metric. Prioritisation of species for protection using Red List category alone, or using the EDGE metric, both recovered FD more quickly than the random allocation of protection among threatened species (Figure 5). Until protection of the 8th species, the lower quartiles of FD recovered by EDGE prioritisation ('worst case scenarios') recover more FD than the equivalent quartiles of using Red List category alone.

4 | DISCUSSION

In this study, we found that crocodylian FD is highly threatened under current extinction scenarios, attributable to phylogenetic clustering of species possessing traits associated with increased extinction risk (e.g. habitat specialisation, low fecundity, reduced ability to withstand climate extremes), and to the high proportion of Critically Endangered functionally distinctive species. Multiple facets of crocodylian diversity are highly threatened, with projected losses of 19%–31% of PD of crocodylians, and 32%–38% of FD, rising to 44% of phylogenetic and 48% of FD if all threatened species were to go extinct. When investigating how to recover maximal FD within the Crocodylia, we found that prioritising species based on

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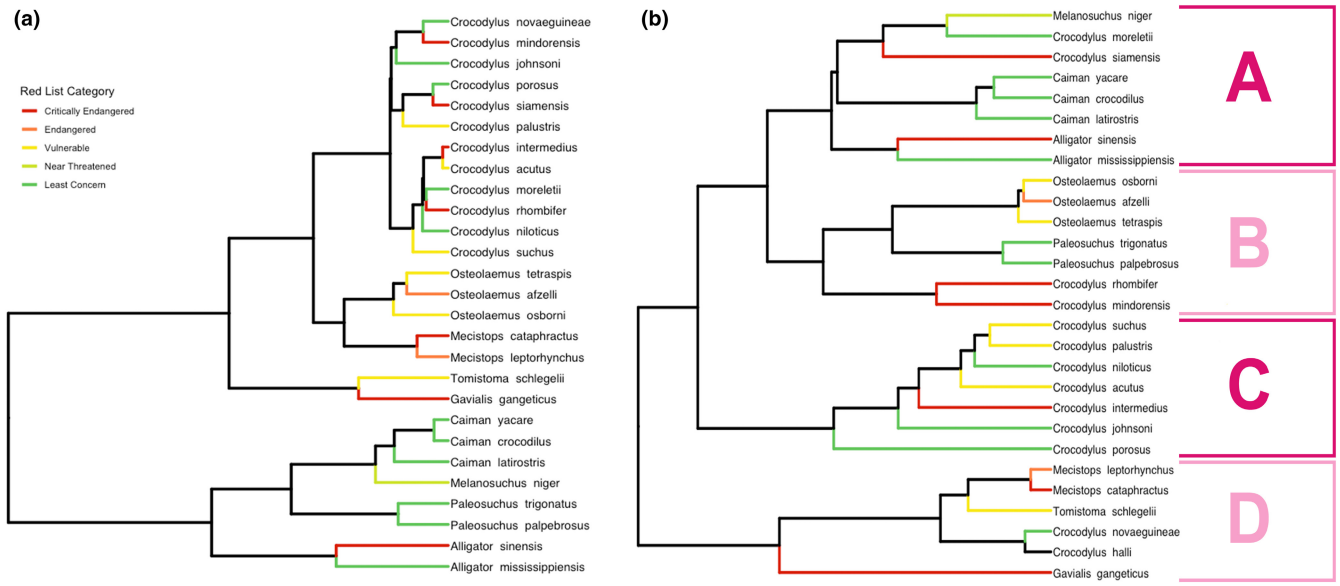

FIGURE 2 (a) Phylogeny of 27 species of extant crocodylian, from the maximum likelihood tree of Colston et al., 2020. Branch tips are coloured by the Red List category of each species, with species that have been split since the most recent assessment awarded their current draft Red List category. (b) Functional trait dendrogram illustrating functional groupings of 28 species of extant crocodylian, branch tips coloured as in the left panel. Functional groupings of crocodylians are illustrated (A–D).

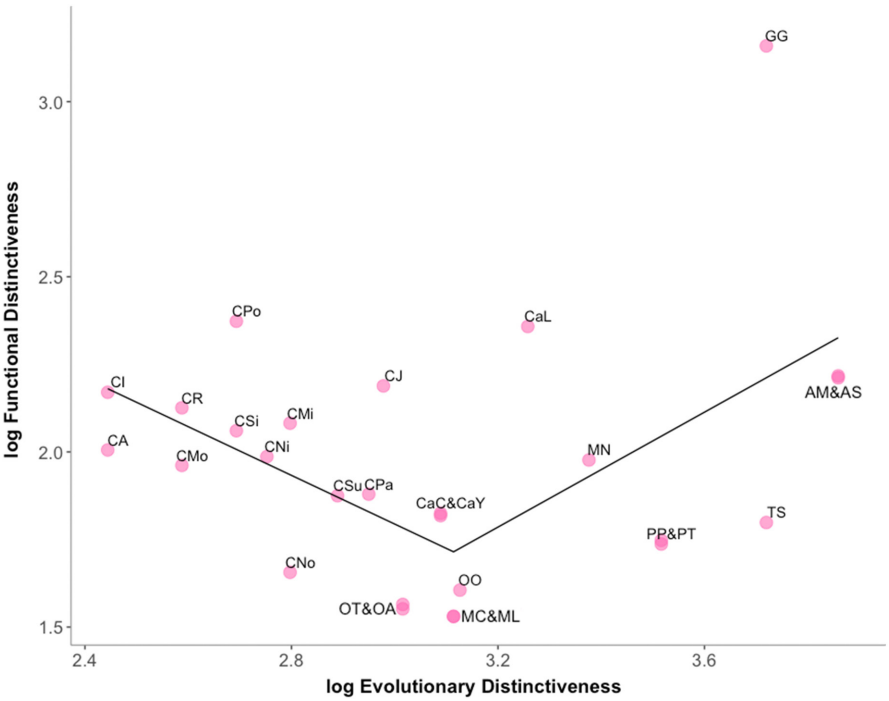

FIGURE 3 Linear relationship with breakpoint at 3.11 between (log) functional distinctiveness and (log) evolutionary distinctiveness ($R^2 = 0.30$). Species abbreviations in Table 1

FUD and risk of extinction was the most successful strategy; in the absence of adequate data on functional traits, prioritising species based on their ED and extinction risk provided a more suitable surrogate for conserving FD than extinction risk alone.

The gharial is the most functionally distinctive crocodylian species (Figure 1), and has extreme values for many traits, including an exceptionally long, thin skull (associated with a diet almost exclusively comprised of fish), a highly aquatic nature, and very large adult sizes (Griffith et al., 2022). Other highly distinctive species include the saltwater crocodile *Crocodylus porosus*, the largest extant species, which is saltwater tolerant; the Chinese alligator and American alligator *Alligator mississippiensis*, which both occur at high latitudes and overwinter at cold temperatures; and the broad-snouted caiman *Caiman latirostris*, which has the broadest of all crocodylian snouts. These distinctive species also exhibit other unusual features that we did not measure, such as the gharial's sexually dimorphic 'ghara' (Figure 1), the long-distance movements of saltwater crocodiles (Campbell et al., 2013), and the communal mound nesting of

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TABLE 2 Minimally adequate model explaining extinction risk in crocodylians using dated phylogeny. Uncorrected (*p*) and Bonferroni adjusted (*p* corr) values are shown.

	Coefficient	*SE*	*t*-value	*p*	*p* corr	Model R^2	λ
Intercept	8.94537	1.20950	7.3958	<0.001		0.5608	0.000
Generality	−0.42579	0.13168	−3.2336	<0.01	<0.01		
RCM	−2.05438	0.45887	−4.4770	<0.001	<0.001		

TABLE 3 Results of univariate pGLS on extinction risk (as defined by Red List category) for the global crocodylian dataset ($n = 27$), with *Crocodylus halli* excluded. Phylogenetic signal (Pagel's λ) of biological traits correlated with extinction risk is reported if λ was significantly different from zero.

Variable	λ	*p*-value of λ	R^2	*t*-value	*df*	*p*-value
Burrow			0.1526	−2.0793	24	<0.05
Aestivation			0.1656	−2.1827	24	<0.05
Generality	0.393	<0.05	0.2641	−2.9344	24	<0.01
Relative Clutch Mass			0.3611	−3.6830	24	<0.01

Abbreviation: *df*, degrees of freedom.

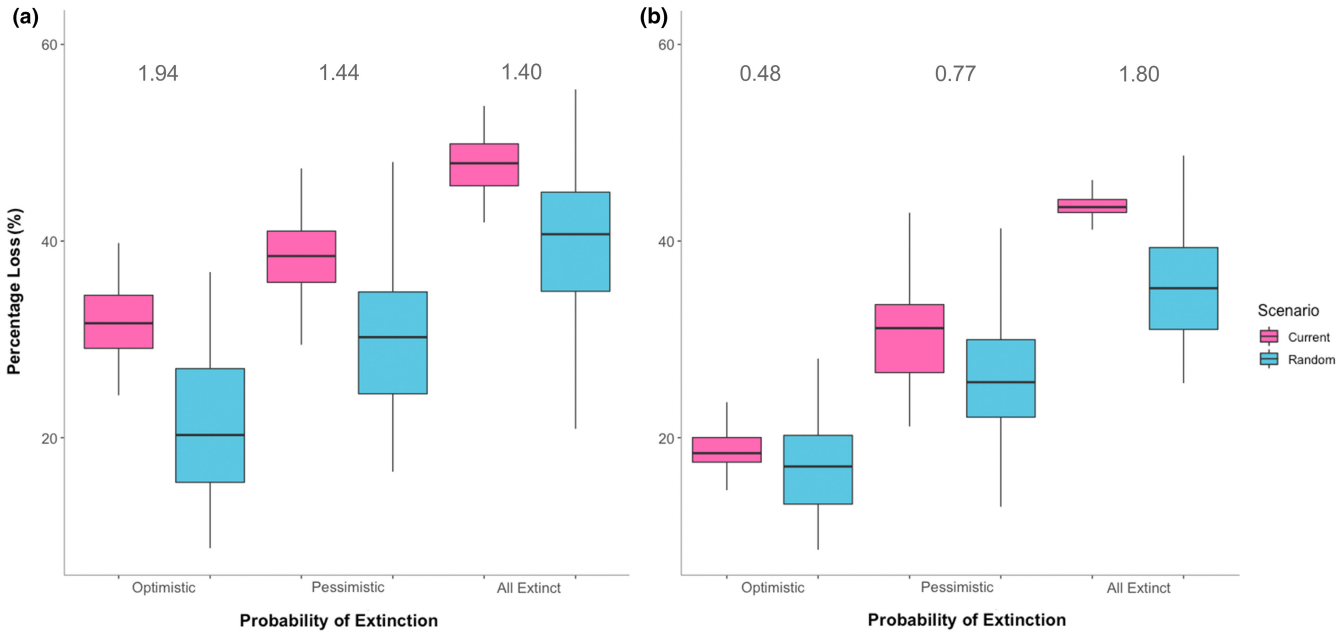

FIGURE 4 Projected percentage loss of (a) functional diversity and (b) phylogenetic diversity in crocodylians. Projections are either optimistic (O) scenarios (where species are assigned the lowest probability of extinction *p*(ext) for their Red List category), pessimistic (P) scenarios (where the highest *p*(ext) for the category is used), or all extinct (a) scenarios (where all threated species are projected to go extinct). Scenarios labelled 'current' assign species to their current Red List category, and 'random' scenarios provide a null model in which the same proportion of threat categories are randomly assigned across species. Numbers above box plots give Hedge's *g* values, indicating effect size for difference between observed and random results, with values over 0.8 indicating a large effect size.

broad-snouted caimans (Larriera, 2002). These additional characteristics suggest that our nominal traits also captured unmeasured functional differences among species.

Of the 10 most functionally distinctive species, six occur in the Asia-Pacific region. Asia is the only continent where all three crocodylian families occur, and is also thought to be where the speciose *Crocodylus* genus originated (Oaks, 2011). We found that this region contained species with the highest and lowest ED. Long periods of unique evolutionary history can drive high FUD, especially through phylogenetic conservatism of traits and trait combinations (Faith, 2015). Rapid diversification in evolutionary radiations can also drive evolution of distinctive trait combinations (Cadotte et al., 2013), and several species of *Crocodylus*, which radiated pantropically over the last ~10 MY (Oaks, 2011), exhibit surprisingly high FUD.

In the Asia-Pacific region, the saltwater crocodile is sympatric with a number of smaller-bodied *Crocodylus* species that are also highly distinctive, which is perhaps an indicator of niche differentiation driven by competition with this large, highly aggressive species. Spatial sorting, the concept of evolutionary change arising as a result of differential dispersal rates at expanding range edges (Shine et al., 2011), may also drive higher rates of diversification in the Crocodylidae (Nicolaï & Matzke, 2019). It has been proposed that species with good dispersal ability (e.g. saltwater crocodile) and

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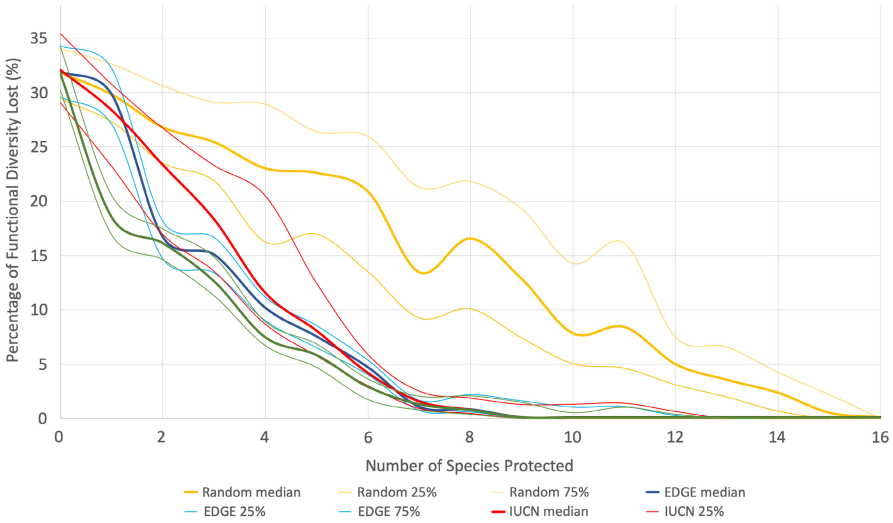

FIGURE 5 Percentage of functional diversity (FD) recovered as species are sequentially protected from extinction according to: Random protected of threatened species (yellow); Evolutionarily Distinct and Globally Endangered (EDGE) metric (blue); Red List alone (red); (d) Ecologically Distinct and Globally Endangered (EcoDGE) metric (green). Steeper accumulation curves indicate more FD recovered per species protected.

species that are no longer at the range expansion front (e.g. Siamese crocodile *C. siamensis*) could speciate from each other due to increased and reduced range expansion potential in these different populations/species (Nicolaï & Matzke, 2019).

Of the 10 highest scoring functionally distinctive species, six are Critically Endangered and are sufficiently depleted as to be functionally extinct in most, if not all, of their range. The EcoDGE scores, based on species' FUD combined with their extinction risk, further highlights Asia as a hotspot of extrinsic threats. Crocodylians occupy inherently fragile habitats such as freshwaters and coastlines, and Asia has exceptionally high human pressures. The average percentage of an Asian crocodylian species' range under high human impact is 18%, versus an average of 0.1%–3% for other continents (2009 Human Footprint Index; Supporting Information, Results). The highest ranked EcoDGE species, the gharial, was historically abundant at very high densities (Lang, 2018), but the species is now absent from over 94% of its historical range, with a concomitant decline in abundance (Lang et al., 2019). The Chinese alligator, Siamese crocodile and Philippines crocodile *Crocodylus mindorensis* are also high priority EcoDGE species; indeed, in Asia north of Wallace's Line, all populations of crocodylians are threatened (Colston et al., 2020).

However, sympatric species also show different responses to similar threats. In crocodylians, we found that threat resilience was linked to fecundity, habitat generalism and ability to withstand climate extremes, relationships also found in other taxonomic groups (Böhm et al., 2016; Lee & Jetz, 2011; Liow et al., 2009). RCM (a measure of fecundity) was the strongest predictor of extinction risk that, when combined with habitat generality in our models, explained 56% of the variation in crocodylian extinction risk. Population recovery following declines will be at slower rates for low-fecundity species, which are less able to compensate for ongoing mortality (Purvis et al., 2000). Depleted populations will remain small for longer, and therefore remain vulnerable to processes including demographic and environmental stochasticity (Caughley, 1994).

These concerns are particularly relevant for crocodylians, as many populations were substantially reduced in the 20th century. While some populations have recovered, others have not. Expensive and intensive reintroduction efforts have met with hugely varying success rates (Grigg & Kirshner, 2015). For example, differences in fecundity may be a key factor in differential establishment of the Cuban crocodile *Crocodylus rhombifer* and invasive brown caiman *Caiman crocodilus fuscus* in the Lanier Swamp, Cuba. Whereas the Cuban crocodile was locally extirpated by hunting following a dedicated reintroduction attempt, the brown caiman established a viable population from a few introduced individuals (Ramos & Rodriguez-Soberon, 2020). Habitat specialisation may also be a factor; our analyses reveal that habitat specialists are at higher risk of extinction, a trend observed across multiple animal taxa (Böhm et al., 2016; Owens & Bennett, 2000). Habitat specialists are more sensitive to habitat loss and degradation, and may be less able to move through marginal habitats to new suitable areas in response to habitat or climate change.

The univariate pGLS also identified that crocodylians that dig burrows and/or aestivate periodically had a lower extinction risk. Such 'sleep-or-hide' traits have been associated with reduced extinction risk in mammals (Liow et al., 2009). These traits may enable such species to persist despite habitat degradation and/or climatic changes by weathering intermittent unsuitable environments, or by enabling individuals to survive long enough to shift to another environment. Understanding traits associated with extinction risk can be useful for conservation. For example, low-fecundity species may respond well to 'headstarting' programmes that boost population levels, whereas species lacking sleep-or-hide traits are likely to respond better to habitat restoration and linkages. Similarly, habitat specialists may serve as good indicator species, as they are more sensitive to environmental changes.

We identified four 'functional groupings' of extant species (Figure 2). Each grouping represents a cluster of crocodylians in trait space with either similar responses to, or effects on, their ecosystem (Hooper et al., 2002). This functional clustering may explain the surprisingly low distinctiveness values for the evolutionarily distinct Sunda gharial *Tomistoma*, which has convergently evolved similar traits (e.g. longirostrine skull, aquatic nature) with the African slender-snouted crocodiles *Mecistops* (Figure 1). Our groupings can

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inform the potential for knowledge transfer between species, including ecological research methods or conservation interventions, and in understanding similarity of ecological roles and broader patterns of convergence in vertebrate evolution.

We found species that shared high extinction risk traits tended to cluster together in functional groupings. For example, grouping D comprises mostly habitat specialists with low fecundity and few sleep-or-hide traits (Figure 2). This clustering of at-risk species, combined with the CR status of many highly distinctive species, leads to our predictions that 32%–38% of crocodylian FD is likely to be lost within 100 years. This is a substantial loss of ecological function for extant crocodylians, and the remaining FD might be even more precarious. Such clustering could lead to 'tipping points' where a functional group persists despite successive species losses, then collapses following the loss of the last remaining group member (Faith, 2015). These results thus support the use of priority-setting approaches that account for co-extinction of similar species, which would prioritise highly threatened clusters of similar species as well as distinctive threatened species, thereby addressing functional complementarity (Faith, 2015).

Uneven distribution of threat status between functional groupings suggests that we may lose whole sets of similar species before we are able to collect empirical data to fully understand their functional roles. Unfortunately, extant crocodylian species already constitute a functionally impoverished subset of pre-human crocodylian diversity. In particular, the arrival or activities of humans is associated with the extinction of the morphologically unusual South-China gavialid *Hanyusuchus sinensis* (Iijima et al., 2022), the endemic Madagascar crocodylian *Voay robustus* (Hekkala et al., 2021), and the Mekosuchinae, an Australasian clade of fully terrestrial crocodylians including a possibly arboreal species (Grigg & Kirshner, 2015). We will likely never know the ecological importance of these species, or whether their geologically recent disappearance has ongoing ecosystem-level consequences (Galetti et al., 2017).

It is vital to prioritise species conservation efficiently in response to ongoing biodiversity declines. However, measuring FD and distinctiveness is challenging, as results depend strongly on initial trait selection, which can be subjective and biased by data availability (Bernhardt-Römermann et al., 2008). Consequently, EcoDGE determinations may not be feasible. Instead, PD, designed to recover evolutionary features across the tree of life, may also capture FD. However, PD assumes that shared traits are due to shared evolutionary histories, whereas convergence can obscure the linkage between PD and diversity of traits; where convergence is high, PD may not necessarily capture the most diverse sets of measurable traits (Kelly et al., 2014), leading some researchers to refer to use of PD to conserve traits as the 'phylogenetic gambit' (Mazel et al., 2018). Our results with crocodylians suggest that using ED to conserve FD would be partially complementary: both metrics prioritise functionally distinctive species that lack close relatives on the tree of life. However, measures of ED will fail to capture those species that are distinct due to rapid evolution.

To assess their usefulness as an aid in real-world assessments, we tested the gain in FD under simulations of four different conservation prioritisation scenarios (EcoDGE ranking, our updated EDGE scores, Red List status alone and random selections of threatened species). The EcoDGE metric swiftly recovered FD, indicating that a ranking based on FUD is a suitable measure for capturing FD within the Crocodylia. Conserving species based on the EDGE metric, or by Red List status alone, also recovered more FD than random allocation. Notably, the 'worst case scenario' (lower quartile and lower limit) of FD recovered by EDGE prioritisation recovered more FD than using Red List status, suggesting that the EDGE metric is a more reliable method for conserving FD than extinction risk alone. In our analysis using crocodylians, the EDGE metric thus appears to perform well at capturing FD, even though the measure is designed to preserve PD.

It is important to recognise that PD-based prioritisation aims to capture the diversity of evolutionary features of species, both measurable and unmeasurable, and so maximise future 'option values' (Faith, 1992). FD is just one part of this diversity. Crocodylian blood has been found to contain antimicrobial peptides which may have future medical uses through anti-tumour and anti-bacterial ability (Chook et al., 2021). These potential uses of crocodylian peptides provide a clear example of an unanticipated value, and conserving crocodylians thus enhances our chances of having such options in the future (Molina-Venegas et al., 2021). Therefore, as has been found in other studies, considering both FD and PD for biodiversity conservation will capture more of the ecological differences, measured and unmeasured, between species (Cadotte et al., 2013; Hidasi-Neto et al., 2015).

Our results show that patterns of FD and extinction risk traits can exacerbate predicted losses of FD. This pattern may, however, also provide a guide to identifying trait differences which could underlie differential responses to threats and conservation actions. Beyond crocodylians, this suggests a functional trait approach could be a useful first step when evaluating conservation actions, and their transferability between species or contexts, and for identifying species that could be utilised as indicator species. These results also suggest that developing an understanding of functional traits and their association with extinction risk may help in predicting threat status of Data-Deficient species. In particular, we found fairly subtle differences in trait values and combinations can lead to different responses to threats. Therefore, conducting such analyses with a narrower taxonomic focus and directed selection of traits may lead to more accurate predictions when aiming to predict species responses to threats or interventions.

Finally, we found that the use of a metric based on FUD and threat status (EcoDGE) to prioritise species for conservation helped recover predicted losses in FD, which supports studies employing similar useful measures such as FUSE (Functionally Unique, Specialised and Endangered; Pimiento et al., 2020). Within the Crocodylia, we identified key species which should be prioritised to maintain global crocodylian FD, with the gharial and Chinese alligator having the highest EcoDGE scores; these two species also have the highest EDGE scores,

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highlighting their importance for global crocodylian biodiversity. However, given the challenges associated with collection of functional trait data, our results suggest that PD-based prioritisations can also capture significant amounts of threatened FD, and continue to be a useful tool in the urgent need to maintain multiple facets of biodiversity.

AUTHOR CONTRIBUTIONS

Phoebe Griffith, Rikki Gumbs and Samuel T Turvey conceived the ideas and designed the methodology; Phoebe Griffith compiled the database: Phoebe Griffith analysed the data with input from Rikki Gumbs and Jeffrey W Lang; Phoebe Griffith led the writing of the manuscript with input from all authors. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

Many thanks to Ashley Pearcy, Christian Foth, Christopher Murray, Igor Roberto, Jeremy Weaver, Jonathan Rio, Kent Vliet, Marisa Tellez and Matthew Shirley for allowing us to use their photos of crocodylian skulls for our landmark analysis. Many thanks to Agata Staniewicz, Lonnie McCaskill, Luis Sigler, Marisa Tellez, Matthew Shirley, Merlijn van Weerd, Peter Taylor, Rom Whitaker, Treya Picking and Xiaobing Wu for sharing their field observations to inform the trait database. We thank NERC and the Oxford Environmental Research Doctoral Training Partnership for studentship and funding (NE/L002612/1). We thank the editorial team and reviewers for hugely helpful comments and suggestions.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data available from the Zenodo repository https://doi.org/10.5281/zenodo.6645415, Griffith et al. (2022).

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How to cite this article: Griffith, P., Lang, J. W., Turvey, S. T., & Gumbs, R. (2023). Using functional traits to identify conservation priorities for the world's crocodylians. *Functional Ecology*, *37*, 112–124. https://doi.org/10.1111/1365-2435.14140

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