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Using indices of species' potential range to inform conservation status

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ABSTRACT

Assessments of conservation status are typically based on short-term extinction risk, but the value of indicators that compare the current state of species (e.g., abundance or distribution) to potential baselines is increasingly recognised. The use of baselines in conservation legislation is hindered by ambiguity in how baselines should be determined and interpreted, leading to inconsistent application. Here, we explored the use of species' potential ranges as a consistent means of quantifying baselines for assessing species' distributions, a key component of conservation status. Using breeding birds of Great Britain (GB) as a case study, we simulated where bird species would be expected to occur today in a modelled world without human land use. We calculated indices that contrasted these potential human-free ranges with realised ranges. Our analyses revealed that 42% of GB birds have wider realised than potential ranges and 28% have narrower realised than potential ranges. These indices could lead to reassessments of current conservation priorities. Eighteen species assigned 'least concern' status by the GB regional IUCN Red List had much narrower realised than potential ranges, suggesting that their ranges are in a more degraded state than currently recognised by Red List criteria. Some of these species are not under active conservation management and could be candidates for higher prioritisation. Our approach provides a systematic means of quantifying range baselines that is not reliant on variable historic data or expert opinion and, thereby, provides a step forward in resolving a major contemporary problem in conservation assessment: how to set baselines in conservation consistently. The insights produced are also of wider scientific and cultural relevance, revealing where species would likely exist today in the absence of historic human impacts. This could be used to identify areas where targeted restoration actions might lead to the return of historically extirpated species, or even to novel colonists.

1. Introduction

Effective and efficient use of conservation resources relies on understanding how and why the abundance and distribution of species change over time. This requires indicators that compare the current state of species (e.g., abundance or distribution) with ecological baselines, or reference states, generally from recent history. Prioritisation of conservation effort is typically guided by comparisons with recent baselines, such as the IUCN Red List of Threatened Species, which places species into broad categories of conservation status based on their short-term extinction risk (IUCN, 2017). It is increasingly recognised that the potential states of species should also be considered as baselines in conservation, revealing how much the current abundance and distribution of species diverge from their potential state in current conditions or in the absence of human pressures (Sanderson, 2006; Redford et al., 2011; Akçakaya et al., 2018; Monsarrat et al., 2019b; Rodrigues et al., 2019).

Comparing the observed and potential states of species can reveal how species have benefited from (Boivin et al., 2016), or been adversely

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affected by (Monsarrat et al., 2019a; Rodrigues et al., 2019), human activities. Such measures can improve our understanding of how anthropogenic processes have shaped ecological communities (Boivin et al., 2016) and indicate what future conservation and restoration goals might be possible (Balmford, 1999; Grace et al., 2019). While returning species to their states prior to any human modification of the environment is obviously unrealistic (Rodrigues et al., 2019), indices based on the potential states of species prior to anthropogenic change offer a more informed basis for the assessment of conservation priorities. Such indices could be used to identify species that currently appear to be at low risk of extinction, but which are much more depleted or range-restricted than they have been in the past. For example, many species of large mammalian carnivores in USA and western Europe are classified as low extinction risk but have not recovered from historical human-driven declines (Chapron et al., 2014; IUCN, 2017). Expectations of the potential abundance (how many should there be?) and distribution (where should they be?) of such species is likely to be much lower than in the past, potentially leading to overestimation of population viability and failure to pre-empt subsequent declines or range retractions. Such species typify the effects of 'shifting baseline syndrome', whereby humans set their expectations based on experience in their lifetime, updating these as their environment changes over time (Pauly, 1995). This psychological phenomenon pervades conservation, including the setting of conservation status (Papworth et al., 2009). Using indices of potential state alongside measures of extinction risk such as the Red List could help to limit the problematic effects of shifting baselines in conservation (Monsarrat et al., 2019b; Rodrigues et al., 2019).

Measures of potential state could help to make assessments of conservation status more systematic. The effectiveness of baselines in conservation legislation can be hindered by unclear guidance on their use (Epstein et al., 2016; Trouwborst et al., 2017). For example, European Union countries are required to maintain selected species at, or restore them to, "favourable conservation status" with respect to their abundance, distribution and habitat (European Commission, 1992) and to report trends in status over 12-year rolling windows (European Commission, 2016). Despite this central role in legislation, surprising ambiguity exists over how baselines for assessing whether species are in a favourable or unfavourable state should be determined and interpreted (Epstein et al., 2016; Trouwborst et al., 2017). Consequently, legislation can be applied inconsistently across different regions due to variation in interpretation of how to deploy baselines, as well as in the timing and quality of baseline data (McConville and Tucker, 2015). This can then fuel conservation conflicts due to different interpretations of the status of wildlife populations (Epstein, 2016). Using potential abundance and distribution as reference states could help to solve these problems.

In this study, we developed a systematic approach for assessing the current state of species' distributions, based on potential range as quantified from species-environment relationships. Species do not typically occupy their entire potential climatically suitable range due to dispersal constraints and historic human pressures such as land cover change and persecution (Gaston, 2003; Svenning and Skov, 2004). Recent approaches have quantified potential range using historic occurrence and fossil data (e.g., Lentini et al., 2018; Grace et al., 2019; Hoban et al., 2019; Monsarrat et al., 2019b), often quantifying historic range at time periods prior to significant human pressures such as European expansion (e.g., 1500) or industrialisation (e.g., 1750; Akçakaya et al., 2018). However, it is challenging to define historic ranges consistently due to taxonomic and regional variation in the timing of human impacts and the sparseness of data on historic species' distributions (Sanderson, 2019; Stephenson et al., 2019). Rather than being tied to specific dates, potential ranges can be defined more conceptually, as the species' distributions expected today in the absence of past human actions (Rodrigues et al., 2019). Such measures would reflect all cumulative human impacts on species' distributions, rather than a subset of impacts over past decades or centuries, and could enable potential range to be assessed consistently across species and regions.

By quantifying relationships between species' distributions and environmental variables, it is possible to simulate how these would be altered in different environmental conditions (Guisan and Zimmermann, 2000). Our goal was to use such simulations to quantify the potential ranges of species under a hypothetical set of environmental conditions that would likely occur now in the absence of land-use modification by humans, and thus in the absence of the anthropogenic processes currently restricting species' distributions. Here, we developed an index that contrasts species' recent distributions to a 'human-free' reference state using model simulations of potential range in a hypothetical environmental scenario. We tested our approach on a well-studied taxon in single geographical region: breeding birds of Great Britain (GB). Extensive human activities such as forestry, agriculture and wetland drainage have reshaped ecological communities in GB over millennia (Simmons, 2001), allowing us to explore potentially large differences in current and potential human-free range. Birds are exceptionally well-monitored in GB (e.g., Balmer et al., 2013) and have been assigned regional IUCN Red List categories (Stanbury et al., 2017), enabling comparisons between our index and a measure of short term extinction risk.

2. Materials and methods

2.1. Data selection

We focused on 229 bird species, comprising 183 species that currently breed in GB and 46 species that do not currently breed in GB but which have done so in the last century (from scientific literature) or are projected to in the future (based on species distribution models – see below). We collated data on the European breeding distributions of all species from Hagemeijer and Blair (1997), which summarises distributions between 1985 and 1988 at c. 50-km resolution (Universal Transverse Mercator [UTM] grid extending to 20-31° East; see Appendix 1). We classified species' presence as the confirmed evidence of breeding, excluding data with only 'possible' or 'probable' evidence from model fitting.

2.2. Model fitting

We used species distribution models (SDMs) to characterise the relationships between species' distributions and environmental conditions. We modelled the probability of occurrence (P_{occ}) of each species in 50-km grid cells across Europe (see Fig. 1). We used SDMs based on bioclimate, topography and land cover variables that have previously been related to bird distributions (Table 1; Fig. S1a). A common criticism of SDMs based upon only climatic variables is that species' distributions are not typically in equilibrium with their climatic niche at fine spatial scales, due to other – often anthropogenic – environmental factors preventing species from occupying climatically suitable areas of their potential ranges (Thuiller et al., 2004). This issue is central to our approach, as we wished to characterise these non-climatic environmental relationships and then simulate species' distributions in the absence of anthropogenic effects such as forestry, agriculture and wetland drainage. See Appendix 1 for a full description of predictors.

We fitted SDMs for each species based on all candidate environmental predictors, using an ensemble of four common techniques: Generalized Linear Models; Generalized Additive Models; Generalized Boosted Models; and Random Forests (see Appendix 1). These model types have been demonstrated to perform well in ensemble modelling frameworks (Bagchi et al., 2013) and to simulate European bird ranges successfully (Stephens et al., 2016). We assessed Europe-wide model performance using AUC (AUC_{EU}), the area under the receiver operating characteristic curve (Manel et al., 2002).
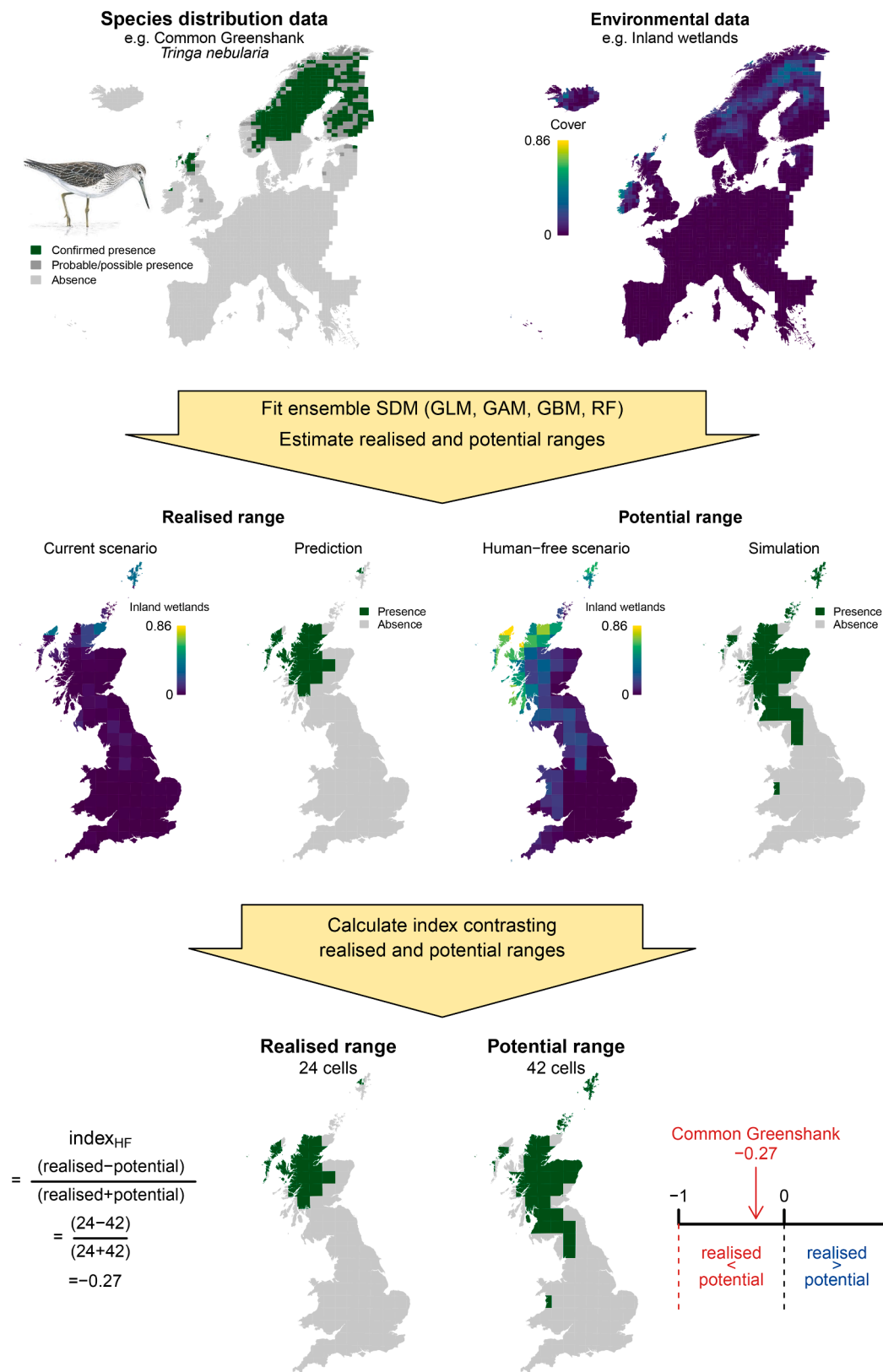
Fig. 1. Our approach for comparing the realised and potential ranges of species, illustrated for the Common Greenshank *Tringa nebularia*. Our procedure includes fitting SDMs using Europe-wide species' distribution data and a suite of contemporary environmental variables (here we illustrate one such variable, inland wetlands, which is a key predictor for this species). The SDMs are then used to predict realised GB range and potential GB range under a scenario of no human land use (wherein the cover of inland wetlands is modelled based on the coverage of suitable soil types). An index contrasting realised and potential ranges, index$_{HF}$, is then calculated. Grid cells are 50-km UTM cells; the spatial scale of distribution data used for SDMs. The illustration of the Greenshank is used with permission from the Royal Society for the Protection of Birds (Mike Langman [rspb-images.com]).

Table 1

The sources and time-periods of environmental predictors used in SDMs.

Predictor type	Predictor	Model fitting	Current GB	Human-free GB
Bioclimate	GDD5	1961-1990[a,b]	1981-2010[a,b]	1981-2010[a,b]
	APET	1961-1990[a,b]	1981-2010[a,b]	1981-2010[a,b]
	MTCO	1961-1990[a,b]	1981-2010[a,b]	1981-2010[a,b]
Topography	High ruggedness	Elevation model[c]	Elevation model[c]	Elevation model[c]
	Low ruggedness	Elevation model[c]	Elevation model[c]	Elevation model[c]
	Coast	Binary coastline	Binary coastline	Binary coastline
Land-cover	Broad-leaved forest	CORINE[2000][d]	CORINE[2012][d]	LPJ-GUESS[e]
	Coniferous forest	CORINE[2000][d]	CORINE[2012][d]	LPJ-GUESS[e]
	Grassland	CORINE[2000][d]	CORINE[2012][d]	LPJ-GUESS[e]
	Moorland	CORINE[2000][d]	CORINE[2012][d]	LPJ-GUESS[e]
	Scrubland	CORINE[2000][d]	CORINE[2012][d]	LPJ-GUESS[e]
	Water bodies	CORINE[2000][d]	CORINE[2012][d]	CORINE[2012][d]
	Inland wetland	CORINE[2000][d]	CORINE[2012][d]	Soil data[f,g]
	Coastal wetland	CORINE[2000][d]	CORINE[2012][d]	Soil data[f,g]
	Pasture	CORINE[2000][d]	CORINE[2012][d]	0
	Arable & cropland	CORINE[2000][d]	CORINE[2012][d]	0
	Built-up area	CORINE[2000][d]	CORINE[2012][d]	0

[a] Harris et al. (2014).
[b] Prentice et al. (1992).
[c] Danielson and Gesch (2011).
[d] EEA (2018).
[e] Smith et al. (2014).
[f] National Soil Resources Institute (2017).
[g] James Hutton Institute (2017).

2.3. Estimating realised and potential ranges

Using our SDMs, we estimated species' near-present day (hereafter 'current') realised ranges and their potential human-free ranges. We quantified realised ranges by predicting P_{occ} in each GB cell under a current environmental scenario (see Table 1). For each GB cell, we calculated an ensemble mean estimate of P_{occ} across 40 models for each species (10 replicates × 4 model-types) weighted by each model's AUC_{EU}. We assessed predictive performance by comparing predicted realised ranges to independent GB breeding distribution data contemporary to the current environmental scenario (2007–2011; Balmer et al., 2013), aggregated to 50 km resolution, using AUC (AUC_{GB}). As with the European distribution data, we did not use GB data with only 'probable' or 'possible' evidence of breeding. We considered models with $AUC_{GB} \geq$ 0.70 to be sufficiently informative to take forward for further analysis (Manel et al., 2002). For species with GB distributions that were near-ubiquitous (absent from only 0–2 cells, 8 species) or highly restricted (present in 0–2 cells, 58 species), and thus for which AUC_{GB} values are likely to misleadingly high, we assessed model fit based on AUC_{EU} (≥ 0.70).

We applied species-specific thresholds that maximised fit between the predicted realised range and distribution data to produce presence-absence predictions. For current GB species, we estimated thresholds by maximising Cohen's kappa statistic (Cohen, 1960), a measure of agreement between sets of categorical data, between ensemble P_{occ} and the independent GB distribution data (Balmer et al., 2013). We used these data so that our predictions were calibrated to the modern distribution data. For species that were very rare or absent from GB (0–2 grid cells), for which we estimated potential range only, we used the European distribution data to estimate thresholds. We used the number of predicted occupied GB cells as our metric of realised range size. We

adopted this approach rather than using observed distributions to represent realised range, to prevent any bias resulting from comparing observed and modelled distributions (where only the latter would be subject to errors in model prediction).

We applied the same models to human-free environmental data to simulate where each species would likely occur in the absence of human effects on land cover (Fig. 1). We developed a 50-km scale human-free environmental scenario for GB based on modern climate (1981–2010) but with current land cover replaced by a modelled alternative in the absence of human processes such as wetland drainage, agriculture, forestry, and industrial and urban development (see Table 1). Appendix 1 gives details of how this human-free scenario, displayed in Table S1 and Figure S1c, was developed; here we provide only a summary. We first estimated the coverage of inland and coastal wetlands for a period pre-dating human drainage, selecting a set of dominant soil types to represent the potential spatial extent of former wetlands, based on the principles of Holliday (2008) (see Table S2). For non-wetland areas we estimated natural land cover (broad-leaved forest, coniferous forest, grassland, moorland and scrubland) using the LPJ-GUESS dynamic vegetation model, run under modern CO_2 levels (400 ppmv) and using a climate data series from 1901 to 1930 to simulate the potential contemporary equilibrium vegetation (following Smith et al., 2014; Table S3).

We used our fitted SDMs to simulate P_{occ} across GB for all bird species under the human-free scenario. We calculated weighted-mean-ensemble human-free P_{occ} using the approach for current ranges, applying the same species-specific thresholds to convert human-free P_{occ} to presence/absence and summing the simulated presences for each species to estimate potential range size.

2.4. Calculating index contrasting realised and potential ranges

We calculated index$_{HF}$, an index that contrasts the sizes of realised and potential human-free GB ranges of current GB species, not considering species that are absent or very rare (≤ 2 GB grid cells):

$$index_{HF} = \frac{(realised - potential)}{(realised + potential)} \tag{1}$$

where realised and potential ranges are the number of 50-km cells occupied in the current and human-free scenarios, respectively (see Fig. 1). This index can vary between 1 and −1, with positive and negative values indicating larger realised and potential human-free ranges, respectively. We used a threshold of 10% to illustrate which species had divergent realised and potential ranges. We classified species with index$_{HF} \geq 0.05$ as favourable (realised ranges at least 10% larger than potential ranges) and those with index$_{HF} \leq -0.05$ as unfavourable (realised ranges at least 10% smaller than potential ranges).

We performed a 'one-at-a-time' sensitivity analysis to test the robustness of the index$_{HF}$ results to uncertainty in the estimation of land cover in the human-free scenario. We adjusted each non-zero land cover in this scenario independently by eight proportions reflecting moderate levels of uncertainty (-20%; −15%; −10%; −5%; +5%; +10%; +15%; +20%). For example, a human-free land cover of 0.50 would be reduced to 0.40 in the −20% scenario. We adjusted the coverage of other land cover proportionally based on the change in the focal land cover. We then simulated potential human-free ranges based on each updated scenario and calculated new values of index$_{HF}$ for each GB species. We compared these results with those based on the standard human-free scenario (see Appendix 2).

We explored the relationship between index$_{HF}$ and GB regional IUCN Red List categories (Stanbury et al., 2017). We combined 'critically endangered' and 'endangered' species into a single category due to the small number of critically endangered species ($n = 7$). We sought to identify species with smaller realised than potential ranges that were not classified as threatened. We compared variation in index$_{HF}$ among Red List categories using a Kruskal-Wallis test and, where required, *post-hoc*

Wilcoxon rank sum tests. We were also interested in which types of species were predicted to have been positively or negatively influenced by human land use. We explored the relationship between index$_{HF}$ and species' UK primary breeding habitat from Balmer et al. (2013; page 130), which categorises species favouring farmland, wetland, woodland, coastal and upland habitat. We classified the habitat associations of 10 previously unclassified species based on expert opinion. Seventeen species associated with mixed or rare habitats were not included in this comparison. We compared variation in index$_{HF}$ among habitat categories using a Kruskal-Wallis test and tested for differences from zero using Wilcoxon signed rank tests.

3. Results

3.1. Model performance

Our models described the 1985–88 European distributions of the 229 study species accurately (mean [10th − 90th percentiles] AUC$_{EU}$ = 0.93 [0.88–0.97]). Using these models, we predicted the distributions of 166 current GB species accurately (AUC$_{GB}$ = 0.93 [0.84–0.99]). We excluded five species with models that performed poorly in GB (i.e., AUC$_{GB}$ < 0.7) from further analysis. See Table S4 for species lists.

3.2. Human-free scenario

The current landscape in GB is dominated by anthropogenic land cover (Table S1; Fig. S1b), particularly arable and cropland (27.1%), pasture for livestock production (26.5%), and grazed moorlands (15.7%). Notably, the coverage of naturally occurring land cover, such as broad-leaved woodland (2.7%), inland wetland (3.2%) and coastal wetland (1.4%) is low. In contrast, our simulated landscape free of human impacts (Fig. S1c) was dominated by broad-leaved woodland (57.5%) but also contained significant areas of inland wetland (18.4%) and coastal wetland (8.6%). Human-free GB was also covered by much less moorland (7%) than modern GB.

3.3. Contrasting realised and potential ranges

We identified 69 out of 166 species with favourable index$_{HF}$ (≥0.05), indicating realised ranges at least 10% larger than potential human-free ranges (see Fig. 2a, Table S4). Fifteen of these species had no potential range in human-free GB and thus index$_{HF}$ values of 1. Fifty species had index$_{HF}$ between −0.05 and 0.05, indicating similarly sized realised and potential ranges. A further 47 species were classified as unfavourable (index$_{HF}$ ≤−0.05), indicating realised ranges at least 10% smaller than potential ranges (see Fig. 2b). Some species had very low index$_{HF}$, including 22 species with index$_{HF}$ ≤−0.2, which indicates realised ranges ≤ two-thirds the size of potential ranges (Fig. 3b). We identified sixteen species that are currently very rare or absent from GB but which had some potential human-free range in GB (Fig. 4). Sensitivity analysis showed that the index$_{HF}$ results were robust to uncertainty in the estimation of land cover in the human-free scenario (Appendix 2).

3.4. Relationship with IUCN Red List

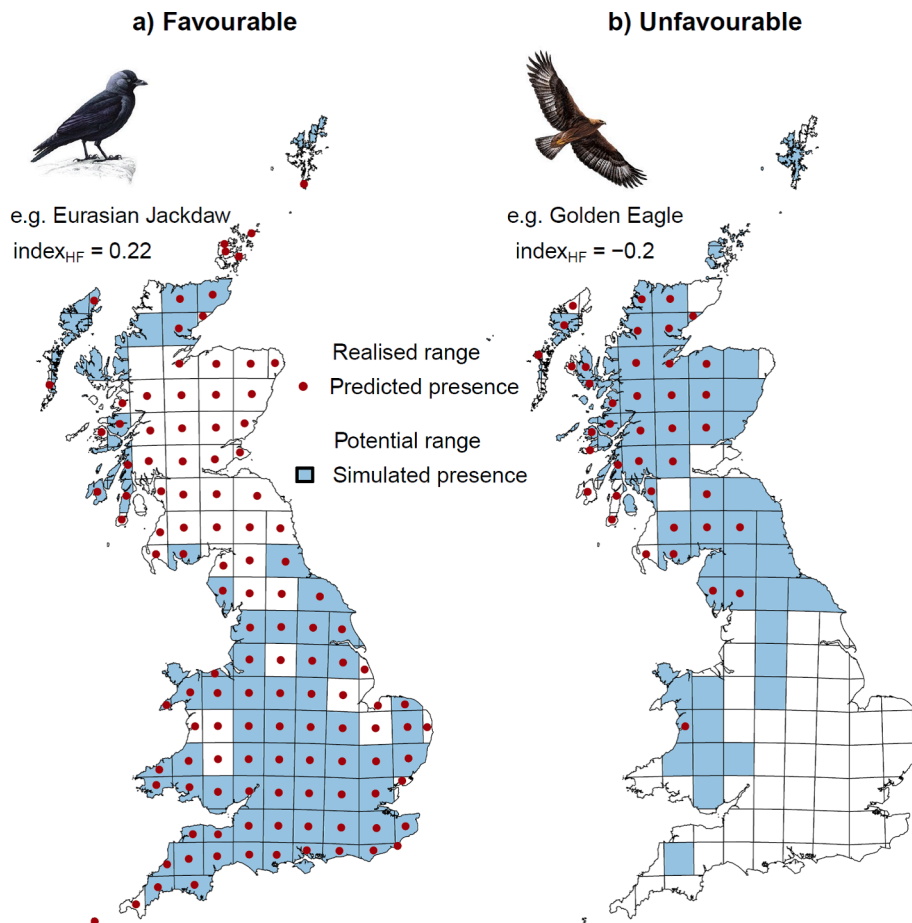While index$_{HF}$ did not differ significantly between GB Red List

Fig. 2. Exemplar species with realised ranges that are a) favourable (Eurasian Jackdaw *Corvus monedula*) and b) unfavourable (Golden Eagle *Aquila chrysaetos*) relative to their potential ranges in a hypothetical scenario without human land use. Grid cells are 50-km UTM cells. The bird illustrations are used with permission from the Royal Society for the Protection of Birds (Mike Langman [rspb-images.com]).
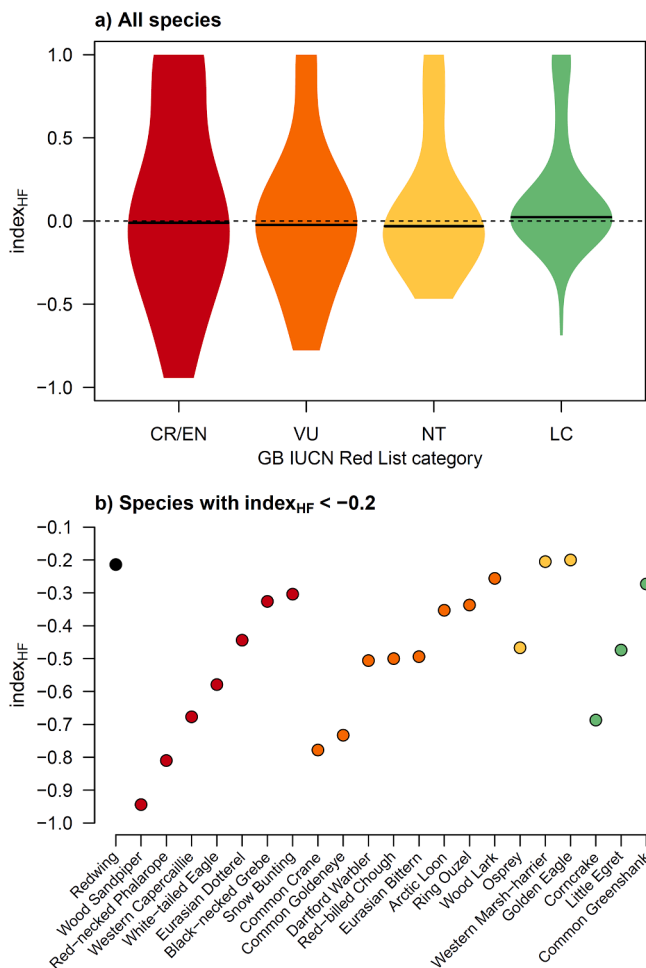
Fig. 3. The relationship between our index contrasting realised and potential ranges (index$_{HF}$) and IUCN Red List category for GB (CR: critically endangered; EN: endangered; VU: vulnerable; NT: near threatened; LC: least concern). In panel a) coloured areas and horizontal bars represent the smoothed distributions and median values of index$_{HF}$ for each Red List category. Values of index$_{HF}$ < 0 indicate that species are predicted to occupy fewer 50-km cells in near-present day (realised range) than contained within their potential range under a hypothetical scenario in the absence of human land use. Values of index$_{HF}$ > 0 indicate larger realised range than potential range. Data are shown for 162 GB species with well-fitting models and GB Red List categories. Panel b) shows index$_{HF}$ values of species with index$_{HF}$ ≤ 0.2, and thus realised ranges ≤ two-thirds the size of potential ranges. Points are coloured by Red List category (CR, black; EN, red; VU, orange; NT, yellow; LC, green). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

categories (Kruskal-Wallis test: χ^2 (3) = 5.11, p = 0.16), there were some interesting patterns across the categories. The least concern (LC) category contained a lower proportion of unfavourable index$_{HF}$ species than the higher threat categories (CR/EN (critically endangered/endangered), 0.37; VU (vulnerable), 0.34; NT (near threatened), 0.42; LC, 0.21). Also, higher threat categories contained species with lower extreme values of index$_{HF}$ (10% quantiles: EN, −0.62; VU, −0.50; NT, −0.20; LC, −0.09). Some non-threatened species had unfavourable index$_{HF}$ (Fig. 3b). Indeed, 18 least concern species were classified as such, including three species with index$_{HF}$ ≤ -0.2, equating to realised ranges ≤ two-thirds the size of potential ranges (Common Greenshank, Corncrake *Crex crex* and Little Egret *Egretta garzetta*). Similarly, three near threatened species (Osprey *Pandion haliaetus*, Golden Eagle *Aquila chrysaetos* and Western Marsh-harrier *Circus aeruginosus*) had index$_{HF}$ ≤ -0.2. In contrast, 21 threatened species (CR, EN or VU) had strongly

favourable index$_{HF}$ (≥0.2), such as the critically endangered European Turtle-dove *Streptopelia turtur*, Garganey *Spatula querquedula*, and Montagu's Harrier *Circus pygargus*.

3.5. Relationship with habitat association

Our index varied significantly with species' habitat associations (Kruskal-Wallis test: χ^2 (4) = 34.5, p < 0.001) (Fig. 5). Most farmland species had wider realised ranges than potential human-free ranges (86% favourable). Farmland species had significantly higher index$_{HF}$ than zero on average (Wilcoxon signed rank test: V = 359, p < 0.001). In contrast, species associated with upland habitat tended to have narrower realised ranges than potential ranges in the absence of human land use (53% unfavourable), having significantly lower index$_{HF}$ than zero on average (Wilcoxon signed rank test: V = 113.5, p < 0.01). The picture was more varied for species associated with coastal, wetland and woodland habitats, with 45%, 27% and 23% of these groups having unfavourable index$_{HF}$, respectively.

4. Discussion

Our study introduces a systematic approach for assessing the status of species' distributions by simulating potential ranges based on species-environment relationships. Our approach provides a step forward in resolving a major contemporary problem in conservation assessment: how to set baselines in conservation consistently (Trouwborst et al., 2017). Following Rodrigues et al. (2019), we used conceptual reference states representing species' ranges that would likely occur now in the absence of past human impacts. Specifically, we use potential species' ranges in a modelled world without human land use, removing any reliance on historical baselines. For the first time, we applied such a baseline to assess the status of many species systematically, calculating an index contrasting the realised ranges of 166 species to their potential human-free baselines. We now discuss the implications of our approach for understanding and conserving wildlife populations.

4.1. Application in status assessments

Comparing our index with the regional Red List for GB revealed several species that were not classified as threatened but occupied much smaller ranges than their potential ranges in the absence of human impacts (Fig. 3). The discrepancy between index$_{HF}$ and Red List category for these species indicates that their realised ranges have been restricted by anthropogenic processes, but they are neither so small, nor so rapidly declining, to be classified as threatened by IUCN Red List criteria (IUCN, 2017). Some of these species are now in the process of population and range recovery as a result of conservation action, but remain heavily conservation-dependent (Gibbons et al., 2011). Examples include Corncrake (dependent on agri-environment management), and Little Egret (benefitting from extensive wetland restoration). Other species, such as Common Greenshank, Golden Eagle and Whinchat *Saxicola rubetra*, are not under active management and may warrant higher conservation prioritisation. The distributions of such species may have first contracted a long time ago and could be much more restricted than understood from recent baselines alone. Species with distributions restricted by historic changes in land cover are thought to be particularly vulnerable to further anthropogenic environmental change (Nogués-Bravo et al., 2014; Estrada et al., 2017) and, thus, may warrant conservation prioritisation. These examples illustrate how shifting baselines can affect our understanding of the potential state of species and subsequently feed into conservation prioritisation. A potential range-based index such as index$_{HF}$ could identify such species, augmenting current Red Listing criteria.

Our approach has parallels with studies that have contrasted current species' distributions to historic distributions from the mid-late 20th century, based on historic distribution and fossil data (Akçakaya et al.,
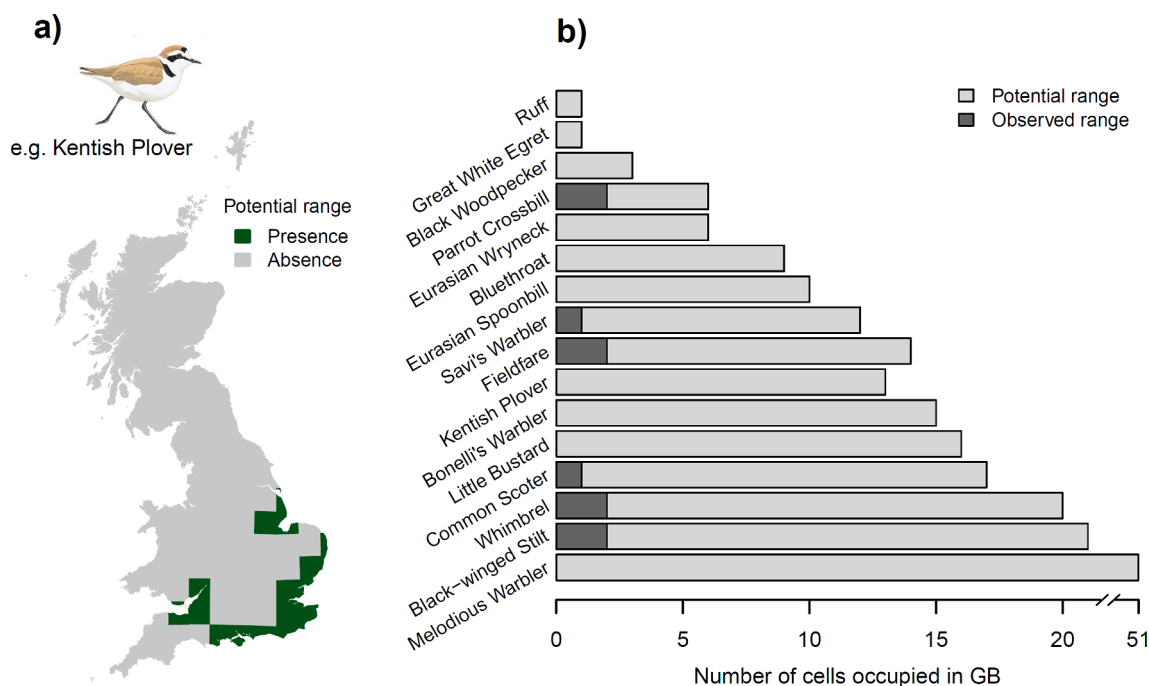
Fig. 4. The potential ranges of species that are very rare or absent from GB. Panel a) shows the potential range of a species currently absent from the GB but that formerly bred here, the Kentish Plover *Charadrius alexandrinus*, under a hypothetical scenario in the absence of human land use. Grid cells are 50-km UTM cells. Panel b) displays the potential human-free ranges of species that are currently very rare or absent from GB (42 other species had zero potential range; see Appendix 1). Where a species was recorded in GB, observed range (dark grey) is shown as a proportion of potential range (light grey). Note that some of the species in b) without observed range have bred in GB in recent years (Great White Egret *Ardea alba*, Eurasian Spoonbill *Platalea leucorodia*, Ruff *Calidris pugnax*, and Eurasian Wryneck *Jynx torquilla*). The Kentish Plover illustration is used with permission from the Birds of Armenia Project.
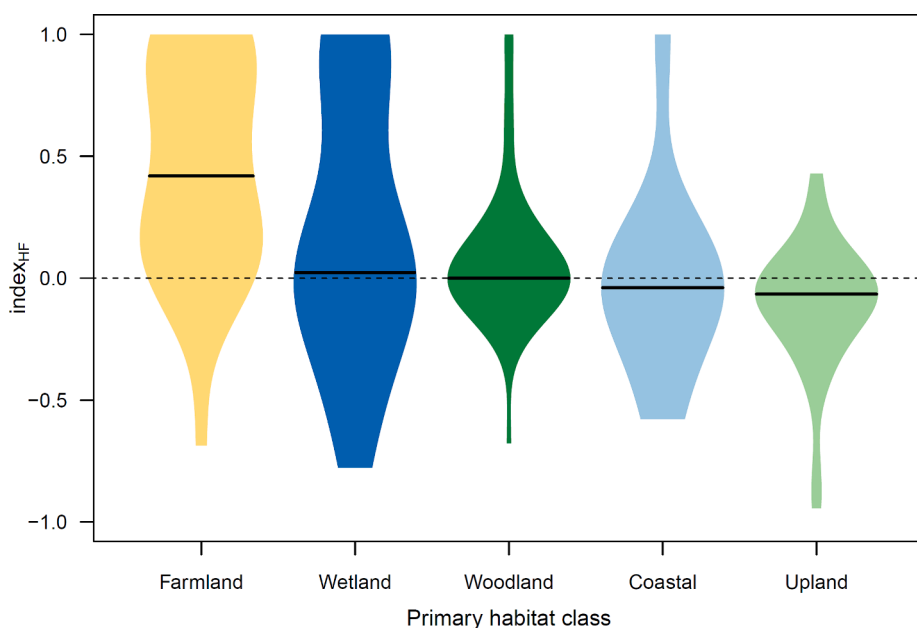

Fig. 5. The relationship between our index contrasting realised and potential ranges (index$_{HF}$) and primary habitat associations from Balmer et al. (2013). Coloured areas and horizontal bars represent the smoothed distributions and median values of index$_{HF}$ for each habitat type. Values of index$_{HF}$ < 0 indicate that species are predicted to occupy fewer 50-km cells currently (realised range) than contained within their potential range under a hypothetical scenario in the absence of human land use. Values of index$_{HF}$ > 0 indicate larger realised range than potential range. Data are shown for 149 GB species with well-fitting models and which were not primarily associated with mixed or rare habitats.

2018; Monsarrat et al., 2019b). Such approaches have been applied to small groups of species (Lentini et al., 2018; Monsarrat et al., 2019b) and are planned for a wider range of taxa by the IUCN Green List of Species project (Akçakaya et al., 2018; Grace et al., 2019). The Green List uses counterfactual and future scenarios to quantify the degree to which species have recovered from defined baselines, in terms of their viability and ecological function throughout their potential range (Akçakaya et al., 2018). It aims to quantify the proportion of species' potential ranges that they currently occupy, based on estimates of historic range

from time periods prior to significant human impact (e.g., 1500 or 1750). Such historic baselines provide valuable insights into human impacts on species ranges over the past half a century but are challenging to apply consistently (Akçakaya et al., 2018; Stephenson et al., 2019). The history of human impacts varies across species and continents, and the more recent the baseline that is used, the greater the extent to which the role of any impacts prior to these dates is ignored (Sanderson, 2019). For example, a species that experienced severe range reductions a hundred years prior to the selected baseline would be

classified as having a narrow historic range, and probably a less ambitious conservation objective. However, there could be just as much restoration potential for such a species as one that declined after the baseline (Sanderson, 2019). Similarly, applying the same historic baseline across continents impacted by humans at different times would introduce systematic bias into the sizes of estimated potential ranges across these regions. Our approach, based on species-habitat relationships under a hypothetical human-free scenario, is not affected by such biases. As such, it provides a step forward in applying baselines consistently in conservation policy, for example, quantification of when species are at favourable conservation status across taxa and geographical regions

Some ecologists have questioned the relevance of indicators based on historic ranges to tackle contemporary conservation problems in a human-dominated world (Kareiva and Marvier, 2012; Robert et al., 2017) and these criticisms are also relevant to indicators, such as ours, that use human-free baselines (e.g., Rodrigues et al., 2019). However, historic or human-free ranges are not intended to be used as targets for recreating the past (Sanderson, 2019). Otherwise we might interpret our index as evidence that farmland bird species should not be a conservation priority despite ongoing declines in most species (PECBMS, 2018). We predicted priority farmland species such as Eurasian Curlew *Numenius arquata*, European Turtle-dove and Grey Partridge *Perdix perdix* to be much less widespread in a non-human landscape in which early successional habitats were rare (Fig. 5). Rather, human-free baselines, which remove all cumulative impacts of human activities, should be used to inform the future based on the past (Sanderson, 2019). Human-free ranges can allow us to understand how human pressures have shaped species' ranges, to monitor the state of species' ranges relative to this consistent baseline and to evaluate how some of the past negative human impacts might be reversed by appropriate conservation action.

4.2. Wider scientific and societal value

Questions of where species occurred prior to human impacts and where they 'should' occur now, are also of wider scientific and cultural significance (e.g., Williamson, 2013). Our study builds on our understanding of how human activities have shaped ecosystems (e.g., Newbold et al., 2016) and species groups (e.g., Monsarrat et al., 2019b), to include the fates of a large number of individual species at a fine spatial scale. For example, the Eurasian Jackdaw *Corvus monedula*, a species that prefers a mixture of open grassland, woodland and urban areas, would probably be much less widespread in the absence of land cover change by humans (Fig. 2a). In contrast, the Golden Eagle, widely considered a species of the uplands and moorlands in GB, would probably be found across a much wider area in the absence of human pressures (Fig. 2b). The fates of these species emphasise the importance of environmental context for understanding the cultural significance of species as well as their conservation, highlighting how shifting baselines can shape our understanding of species' distributions.

Our model simulations suggest that human-free GB would be more suitable for upland species, but less so for many farmland species (Fig. 5). Species associated with uplands tended to have restricted realised ranges despite humans having created a greater area of moorland habitat. This may reflect negative effects of long-term, extractive human use of moorlands by grazing, burning, hunting and forestry (McVean and Lockie, 1969). Surprisingly, species associated with woodland were not predicted to have wider distributions in the woodland-dominated human-free scenario (see Fig. S1c). However, the woodland species group includes many species associated with woodland fringes and parkland, which are likely to prefer fragmented woodland habitats. Species associated with closed canopy woodland are more likely to have smaller realised ranges than potential ranges, such as Northern Goshawk *Accipiter gentilis* (-0.19) and Western Capercaillie *Tetrao urogallus* (-0.68). Given the debate over whether lowland Europe was covered by wood-pasture or closed canopy forest (e.g., Birks, 2005),

future work could explore the influence of alternative scenarios of broad-leaved forest in baseline scenarios. Indeed, our sensitivity analysis revealed that our indices were generally robust to moderate levels of uncertainty in human land cover, but that perturbations in the coverage of broad-leaved woodland – the dominant land cover in human-free Great Britain – were most likely to influence index$_{HF}$.

A number of species with potential range across GB in the human-free scenario are currently very rare or absent (Fig. 4). For example, the Kentish Plover *Charadrius alexandrinus* bred in GB up to the second half of the 20th century, with its extirpation linked to persecution and disturbance in its coastal habitat (Balmer et al., 2013). Simulated human-free ranges could identify areas where targeted habitat and species restoration actions might lead to the return of historically extirpated species, or even to novel colonists. Previous approaches have characterised historic ranges to evaluate where to allocate conservation effort to restore species to areas of their potential range (Lentini et al., 2018; Monsarrat et al., 2019b). Our approach would be particularly suitable for this aim as it can identify areas that are climatically suitable but where habitat may have been degraded by human activities. It is unclear how extirpated or potentially colonising species should be treated by regional conservation status assessments or prioritisations. However, if species are removed from regional conservation status assessments once they are lost from a region, as is the case for bird species lost from the UK such as the Kentish Plover (Eaton et al., 2015), it is too easy for them to slide quickly from the consciousness of conservationists and the public.

4.3. Is there a role for unbiased baselines?

Although we performed our assessment on a single region, our method could be generalised to any region (or period, past or future) and taxon for which species' distributions are known and human-free scenarios can be simulated. Our study is the first attempt to apply potential range baselines to many species. There are obvious challenges to applying a standardised approach to describe the distributions of species with varied ecological requirements. Ongoing discourse with policy-makers will be vital to ensure that our approach for defining baselines in conservation can be refined into a practical policy tool.

We targeted an approach that could be easily generalised to other systems. As such, we used the same predictor variables for all species and used standard performance metrics to assess model validity. This approach could be modified by fine-tuning models to the ecological requirements of individual species. Selecting different sets of variables for each species could help to resolve the issue of poorly fitting models (of which we excluded five from our analysis). Also, evaluating the ecological realism of the fitted species-habitat relationships could help ensure that simulations of potential range are based on sensible relationships and are not subject to spurious correlations between predictor variables. However, such modifications would probably require expert opinion, introducing subjectivity and potentially an effect of shifting baselines in the expected habitat preferences of species (Anderson et al., 2009). Here, we assessed model validity based simply on fit, measured by AUC, to contemporary distribution data (both the fitted data and independent data). Future work could consider different ways of assessing model validity, including a variety of fit metrics. Such decisions depend on the balance sought between wide applicability and model optimisation.

Another feature of our approach that could be refined is the treatment of model uncertainty. We incorporated uncertainty implicitly, calculating ensemble predictions across 40 models per species (10 replicates × 4 model-types). We then produced a single value of index$_{HF}$ for each species, from which the status of a species could be assessed unambiguously. Uncertainty in index$_{HF}$ could be estimated explicitly by quantifying index$_{HF}$ independently from each model, from which estimates of central tendency and spread could be derived. This would provide policy-makers with more information on the uncertainty

underlying each species' index, but would increase the complexity of interpretation.

Modelling should be performed at the finest spatial scale at which reliable data on species distributions and environmental variables are available, to ensure that fine-scale effects of land cover on species' absences are not obscured. Finer scale modelling would have been preferable in our GB-scale study, however the environmental variables required to simulate human-free scenarios (e.g., coarse resolution dynamic vegetation models) precluded such an approach. Developing realistic human-free scenarios would probably be the most challenging aspect of applying our approach in other contexts. Various studies have generated maps of potential landcover prior to human impacts over large areas by combining landcover data, models of landcover suitability and expert knowledge, suggesting that this goal is attainable (e.g., Wuyts et al., 2017; Nomura et al., 2019).

Clearly, spatial distributions are only one characteristic of species' ecology contributing to conservation status. Our approach could be extended to evaluate baselines for population size by fitting models to abundance data (e.g., Howard et al., 2014). Predictions of potential abundance could be combined with minimum thresholds for favourable population size, estimated based on risk of population decline (Green et al., 2020), to determine where viable populations could exist. However, our range-based metric is designed as an easily applied proof-of-concept, with wide applicability. Our approach provides a means of assessing range baselines for ongoing conservation, and potentially also for reintroductions, that is not reliant on recent baselines or variable historical records. This could facilitate a level playing field for setting conservation baselines in areas that have little historical species data, as is the case for many of the world's most biodiverse areas.

CRediT authorship contribution statement

Tom H.E. Mason: Conceptualization, Methodology, Formal analysis, Validation, Writing - original draft, Writing - review & editing, Visualization. **Philip A. Stephens:** Conceptualization, Methodology, Writing - review & editing, Funding acquisition. **Gillian Gilbert:** Conceptualization, Writing - review & editing, Funding acquisition. **Rhys E. Green:** Conceptualization, Writing - review & editing, Funding acquisition. **Jeremy D. Wilson:** Conceptualization, Writing - review & editing, Funding acquisition. **Kate Jennings:** Writing - review & editing. **Judy R.M. Allen:** Formal analysis, Writing - review & editing. **Brian Huntley:** Methodology, Writing - review & editing. **Christine Howard:** Methodology, Writing - review & editing. **Stephen G. Willis:** . : Conceptualization, , Methodology, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.107343.

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