Anthropocene refugia: integrating history and predictive modelling to assess the space available for biodiversity in a human-dominated world

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1. Abstract

During periods of strong environmental change, some areas may serve as refugia, where components of biodiversity can find protection, persist and potentially expand from should conditions again become favourable. The refugia concept has previously been used in the context of climatic change, to describe climatically stable areas in which taxa survived past Quaternary glacial-interglacial oscillations, or where they might persist in the future under anthropogenic climate change. However, with the recognition that Earth has entered the Anthropocene, an era in which human activities are the dominant driving force on ecosystems, it is critical to also consider human pressures on the environment as factors limiting species distributions. Here, we present a novel concept, Anthropocene refugia, to refer to areas that provide spatial and temporal protection from human activities and that will remain suitable for a given taxonomic unit in the long-term. It integrates a deep-time perspective on species biogeography that provides information on the natural rather than current-day relictual distribution of species, with spatial information on modern and future anthropogenic threats. We define the concept and propose a methodology to effectively identify and map realised and potential current and future refugia, using examples for two megafauna species as a proof of concept. We argue that identifying Anthropocene refugia will improve biodiversity conservation and restoration by allowing better prediction of key areas for conservation and potential for re-expansions today and in the future. More generally, it forms a new conceptual framework to assess and manage the impact of anthropogenic activities on past, current and future patterns of species distributions.

Keywords: Anthropocene, ecosystem restoration, refuge, rewilding, shifting baseline, species distribution modelling

2. Introduction

While species distribution patterns have strong signatures tied to natural biotic and abiotic processes, it is becoming increasingly difficult to ignore the role that humans play in shaping the composition of species assemblages across landscapes. With 95% of land having at least some degree of modification by human activities [1], the extent of wilderness areas have declined dramatically, and so have the opportunities to protect and conserve viable populations of many species in their natural habitat. Meanwhile, anthropogenic climate change is predicted to cause range shifts, range contractions and changes in elevational distributions in many organisms [2,3], challenging our approach to biodiversity conservation [4]. Human impacts on the global environment have become so pervasive that a new geological epoch has been proposed: the Anthropocene [5]. Identifying the space available for biodiversity protection and recovery in this human-dominated world is a challenge that requires a comprehensive understanding of the interactions between species' natural biogeographic patterns and the spatial distribution of anthropogenic pressures.

The terms 'refuge' or 'refugia' are commonly used to refer to areas where components of biodiversity retreat to, and persist in, under increasing environmental stress, with the potential to re-expand once the stress decreases [6,7]. These concepts have previously been applied in the context of past or contemporary climatic change, to identify areas that are relatively buffered from climatic changes and where components of biodiversity have persisted in the past or may be able to persist in the future. Such areas can act as sources of recolonization when environmental conditions improve, often have long-lasting imprints on species distributions [8], and have therefore become a central focus in much biogeographic research [6]. However, previous uses of the concept have not accounted for the impact of anthropogenic pressures, other than climate change, on species' biogeographic patterns [6]. With the recognition that human activities are now a major force driving global ecosystems [9], there is a need for incorporating a wider range of human pressures, beyond anthropogenic climate change, as drivers limiting the persistence of species in human-dominated landscapes.

Here, we build on previous uses of the term to introduce a novel concept - Anthropocene refugia - which refers to areas allowing the long-term survival and persistence of organisms that are sensitive to human activities and providing sources for broader recovery if pressures are decreased. It intersects knowledge on the potential distribution of the organism of interest, incorporating prehistoric and historic data on a taxon's past distribution, with spatially explicit information on current and future anthropogenic pressures. The outcome is the identification of areas where an organism can persist, or be restored to, in the Anthropocene, given its ecology, vulnerability to human activities and the predicted changes in suitability of these areas. This concept will contribute to a much-needed development of more proactive approaches to nature conservation to overcome ongoing species and ecosystem declines and long-term reductions in biodiversity [10,11]. We define this novel conceptual framework and suggest a methodology to identify Anthropocene refugia in practice, identifying the sources of information and available material that can be used for this exercise. We also discuss the applications for species' conservation, management and restoration, using examples for two megafauna species as case studies and proof of concept.

3. Anthropocene refugia: a conceptual framework

The concept of refugia was originally used to study the response of organisms to past periods of glacial-interglacial oscillations of the late Quaternary [6], allowing a greater understanding of observed patterns of species' biogeography, evolution and demography [e.g. 12–14]. More recently, the term climatic refugia has been applied to contemporary landscapes, referring to locations projected to harbour remnants of present-day climates, which may serve as safe havens for biodiversity under future climate change [7]. In conservation planning, identifying these climate change refugia can help prioritise management efforts in the face of contemporary climate change [15,16].

These definitions, however, only consider climate as the driver of change in species distribution and abundance, both in evolutionary and ecological timeframes [16]. While changes in species' biogeography during the Quaternary were largely driven by glacial-interglacial oscillations [17], the more recent use of

83 climate change refugia fails to incorporate anthropogenic pressures that, along with climate change, can
84 affect the distribution of species in an increasingly human-dominated world. The concept of Anthropocene
85 refugia overcomes this limitation by incorporating climate change and a wide range of anthropogenic
86 pressures into the identification of refugia. It designates a spatial entity that answers to two qualities: being
87 ecologically suitable for the biodiversity unit considered and having relatively low levels of observed and
88 predicted human pressure to allow its long-term (through several generations) persistence in this area
89 (Figure 1). We differentiate realised and potential refugia, based on whether the refugia are within the
90 taxon's current range, or within the area where it could potentially persist in the future.

91 Anthropocene refugia are different from "remnants", patches of suitable habitat for species intolerant to a
92 human-modified landscape [18], or "coolspots", areas across species distributions that are free from
93 anthropogenic threats that the species is sensitive to [19], which are both snapshots in time of where
94 species can persist within their current range. In the Anthropocene refugia concept, a strong emphasis is
95 made on identifying the potential range of species, taking into account the natural rather than current-day
96 relictual niche of the species, and the stability of suitable habitat through time. Niche truncation caused by
97 past local extirpations biases our understanding of natural habitat-species relationships. By
98 underestimating the extent of potential suitable habitat, this can affect our understanding of areas
99 available for conservation today [20] and provide unreliable forecasts of distribution changes under future
100 climate change [21]. This case of shifted baseline can be avoided by incorporating prehistoric and historic
101 data on the taxon's occurrence into estimates of potential distribution. As such, this concept bridges
102 perspectives on taxa's long-term biogeography with current and future predictions of distribution patterns
103 in human-dominated landscapes.

104 Anthropocene refugia can be considered both conceptually and as a tool for conservation and
105 management. The Anthropocene refugia concept allows higher-level thinking about the implication and
106 consequences of human activities on species distribution and about the space available for biodiversity in

the Anthropocene. Similar to the concept of glacial-interglacial refugia, which allows for a critical examination of current biogeographic patterns with a historical perspective, the identification of Anthropocene refugia will equip the next generations of ecologists with a tool to understand how biogeographic patterns emerge in a human-dominated world. It combines the protection perspective with the restoration (reintroduction or rewilding) perspective, in contrast to more classic conservation approaches which focus on the former [22].

As a tool, Anthropocene refugia can be used in categorisation, decision making, and inference for conservation planning. The approach is complementary to previous efforts to identify priority regions for establishing protected areas or remaining wilderness areas [1,23], but acknowledges that species persistence does not only rely on the existence of formally protected or pressure-free areas [24]. Although protected areas are most certainly a critical component of large-scale conservation planning efforts, some species have demonstrated their ability to tolerate substantial levels of human pressures and survive outside of formally protected areas [25,26]. By enabling persistence, acting as wildlife corridors and serving as a source for future recolonization, refugia are critical to support biodiversity protection in a changing world. Compared to previous efforts to map human footprint [27] or degree of human modification [1], which provide information on the current distribution of human pressures, Anthropocene refugia can incorporate a finer taxonomic resolution, by intersecting these types of information with distribution data for a given taxon. Because individual taxonomic units – populations or species – are often regarded as the fundamental unit of conservation, this makes it a valuable new tool to inform conservation management.

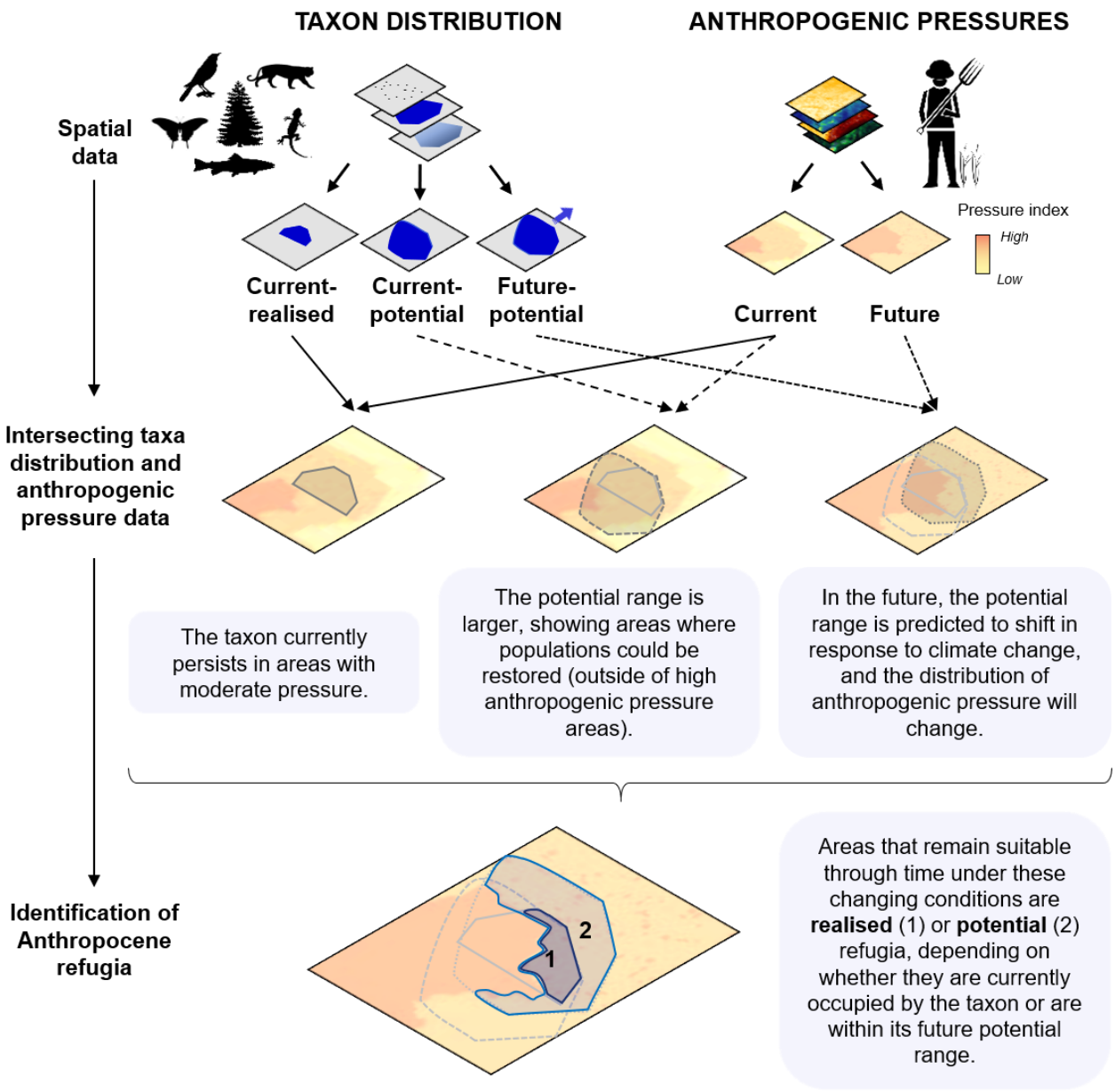


Figure 1. Schematic representation of the Anthropocene refugia concept. Spatially-explicit data on taxon distribution (point data, range maps or predicted distributions) and anthropogenic pressures are combined to map the distribution of realised and potential Anthropocene refugia.

4. Identifying Anthropocene refugia

In practice, mapping Anthropocene refugia requires geographic information on the long-term distribution of the taxa of interest and of the relevant anthropogenic pressures (Figure 1). We provide suggestions below for the type of data that could be included and identify some online and open-access datasets from which this information can be retrieved (Supplementary Information).

135 ***Taxon distribution data***

136 Distribution of taxa can be mapped from 1) point data, the locations where a species has been recorded, 2)
137 geographic ranges, the geographic boundaries of the area where a species is known to occur [28] and 3)
138 predicted distributions, the areas where a species is likely to be present as inferred from the suitability of
139 environmental conditions [29]. We refer the reader to existing reviews to understand the attributes,
140 strength and limitations of these different data types in the context of conservation [29–33].

141 To be useful in mapping Anthropocene refugia, point data need to be transformed into areas, e.g. by
142 intersecting them with geographic units (grid squares or administrative boundaries) or by converting them
143 into geographic ranges (extent of occurrence EOO or area of occupancy AOO [31]), using interpolation and
144 expert knowledge. Predicted distributions that relate species occurrence with environmental conditions
145 based on mechanistic (process-based) or correlative (statistical) niche modelling enable the extrapolation of
146 incomplete point locality data, and the interpolation of habitat suitability measures throughout the range
147 [34,35]. They can provide a more realistic outcome by minimising both commission and omission errors
148 (erroneous indication that a species is present or absent, respectively), but require following high standard
149 practices regarding the choice of species distribution data or mechanistic links describing species' niche,
150 environmental predictors, and the building and evaluation of the model [36]. Mechanistic and correlative
151 niche models can also be used to predict changes in taxon distribution under future scenarios of climate
152 change [37,38]. From these, hypotheses about the future extent of occurrence of organisms can be derived
153 to inform conservation interventions [e.g. 39], and serve as a basis for mapping Anthropocene refugia.

154 Niche-truncation caused by past or current anthropogenic impacts may bias our understanding of species'
155 biogeography and ecological requirements [20,21]. This in turn can lead to underestimating the potential
156 distribution of species and the area available for their conservation [20,40] and bias forecasts of species
157 distribution under future climate change [21]. The distribution data used in the mapping should be
158 informative of the natural rather than current-day relictual range of species, to counter the undesirable

159 effects of the shifting baseline syndrome [41]. This may require a deeper investigation of past local
160 extinctions and truncations in species-environment relationship, which may be informed by integrating
161 knowledge or data on the historical distribution of the species [42].

162 Long-term biodiversity data, i.e. prehistorical and historical occurrence records collected from
163 archaeological, museum, written and oral sources, can fill gaps in knowledge and inform the natural
164 distribution of organisms, i.e. the range they could occupy today in the absence of human impacts. Fossil
165 records of the late Quaternary can provide information on biodiversity changes as a result of climatic changes
166 and anthropogenic impacts over the last millennia, while historical descriptions and museum specimens
167 collected by literate travellers and naturalists are informative of the more recent past, particularly of the
168 period following European expansion. Finally, traditional ecological knowledge accumulated through many
169 generations of close interactions between people and the natural world can provide local information on the
170 state of ecosystems from the relatively recent past [43]. Ultimately, the temporal cut-off for long-term
171 biodiversity data should be taxon-specific and reflect the timeline and geography of known or suspected
172 impacts as well as the objectives of the study.

173 If past climate data are available, a multi-temporal calibration approach to identify a taxon's potential niche
174 from past and present occurrence records can be used to project the range in current environmental
175 conditions using niche modelling [e.g. 39,56], assuming that the niche has remained stable through time [45].
176 For data-poor regions or taxa, expert knowledge can also bring a useful approximation to the potential
177 natural range of the organism. Finally, a combination of different approaches can prove the most efficient to
178 infer the biogeographic history of species and deduce their current potential range [46,47].

179 In general, the use of long-term data in ecological analyses is increasing, with positive outcomes to improve
180 our understanding of natural species-habitat relationships and reduce the pervasive effect of the shifting
181 baseline syndrome. As an example, Lentini et al. reconstructed the historical distribution of kākāpō S*trigops*
182 *habroptilus* using a combination of Holocene fossil records, mid-Holocene climate data and species

183 distribution modelling, identifying areas suitable for reintroductions for this Critically Endangered bird
184 species [44]. Laliberte and Ripple used historical data to identify patterns of range contraction and expansions
185 in 43 species of North American carnivores and ungulates, and showed reduced persistence of species in
186 areas of higher human influence following Euro-American settlement [48]. These types of studies can form
187 the basis of Anthropocene refugia mapping for the taxa they are considering.

188 All data types are prone to error, incompleteness and biases (temporal, geographical, environmental and
189 taxonomic), which can affect interpretation of distribution patterns. Biases in the Holocene fossil record are
190 examined by Crees et al. in this special issue [49] and discussion on the biases and errors in data extracted
191 from the historical literature and museum specimens can be found in [50–52]. Historical data, while powerful
192 in their potential to highlight neglected aspects of species' biogeography, require a rigorous methodology for
193 their collection and interpretation to avoid the common pitfalls in historical ecology [53]. Before including
194 long-term data in analyses of species distribution, sources of errors and biases should be thoroughly
195 investigated and corrected for, and the remaining uncertainties acknowledged.

196 We list examples of online repositories for global species distribution data, including archaeological
197 records, in Supplementary Information. Each of these data sources need to be critically evaluated for their
198 relevance to answer biological questions, according to criteria such as resolution, scale or
199 representativeness of natural range.

200 ***Anthropogenic pressures***

201 The anthropogenic pressures to include in the mapping are those that directly or indirectly have a negative
202 impact on the persistence of the organism of interest and will vary according to the taxon considered and
203 the spatial scale of the study. For example, while land mammals are mostly affected by habitat loss,
204 degradation and harvesting [54], reptiles and amphibians appear to be primarily affected by agriculture and
205 biological resource use, urban development, natural system modification, invasive species and infectious
206 diseases [55,56], and megafaunal species across taxonomic groups are mainly threatened by direct

harvesting [57]. Salafsky et al. [58] proposed 11 categories of threats in a unified classification that is being used by the International Union for the Conservation of Nature (IUCN) Red List [59]. It can prove a valuable resource, along with a literature review or expert knowledge, to identify the set of threats that is relevant to the organism of interest.

Recent studies have also used primary data sources on human stressors to build indices of global cumulative impact of human activities on the environment. The Human Footprint project uses for example data on 1) built environments, 2) population density, 3) electric infrastructure, 4) crop lands, 5) pasture lands, 6) roads, 7) railways, and 8) navigable waterways to map the direct and indirect human pressures on the environment globally in 1993 and 2009 [27]. In a recent study, Kennedy et al. [1] provide a cumulative measure of human modification of terrestrial lands based on 13 anthropogenic stressors classified in five major categories: 1) human settlement, 2) agriculture, 3) transportation, 4) mining and energy production, and 5) electrical infrastructure, for a median year of 2016. Spatially explicit global datasets for these two projects are available online [60,61] and are relevant resources that can be used for mapping Anthropocene refugia.

With the growing development of remote-sensing technologies [68], global environment modelling and systematic surveys, spatially-explicit information on current anthropogenic pressures is increasingly made available through publicly available online repositories. We provide a non-exhaustive list of these spatial datasets for different types of human pressures in the Supplementary Information, which can serve as a basis for more case-specific listing of potential data sources. If spatial information for some of the identified threats is unavailable, proxy variables that correlate with the variable of interest can be considered for replacement. The methodology can also be revisited to include additional pressures as more data become available in the future.

New and emerging threats from wildlife trade, changing land use patterns, and the increase in global human populations, may increase pressure on ecosystems in the future. On the other hand, the creation of new

protected areas and farmland abandonment may provide additional space for biodiversity [62,63]. In order to identify which areas will allow the long-term persistence of a given organism, these future dynamics need to be incorporated, as much as possible, into the mapping of Anthropocene refugia. Spatially-explicit forecasts of future human population [64], urban expansion [65], global habitat conversion [66] and deforestation [67] are readily available and can be used as a first approximation to understand how the distribution of anthropogenic pressures will change in the future. These datasets however summarise future risks at coarse scales and for different points in time (e.g. from a decade in the future for deforestation risk to a hundred years for human population density), making it a challenge to reconcile them into a single map and to use them as a basis for decision-making at the local scale. Socio-economic, political and ecological trajectories as well as the interactions and retroactive feedbacks between them are generally challenging to model, hindering our capacity to obtain robust predictions of the future distribution of anthropogenic pressures. Given the importance of such predictions for implementing effective conservation and policy measures, the development of methods to produce robust and spatially explicit predictions of the distribution of human activities under different scenarios and over relevant timeframes is an important focus for future research. Release of these predictions in open access format will be critical to improve our ability to identify Anthropocene refugia.

Mapping Anthropocene refugia

Assigning relative pressure scores to each human pressure variable and intersecting these with species distribution data will result in a taxon-specific map of anthropogenic pressure intensity within the range of the species. Anthropocene refugia lie at the intersection of areas that remains suitable for the organism through time and areas with low levels of observed and predicted anthropogenic pressure. A distinction is made between “realised” refugia that are currently occupied by the organism of interest and predicted to remain suitable in the future, and “potential” refugia, i.e. areas where the taxon is not currently extant but that are within its potential future range under scenarios of future climate change, future human-driven landscape change, and other predicted anthropogenic pressures.

Using thresholds to convert maps of continuous value into binary maps highlighting the specific areas that could act as Anthropocene refugia may be useful for management and decision-making purposes. This approach however leads to loss of valuable information and should be used with caution. If necessary, an option is to calibrate the threshold based on the level of threat that the organism is currently able to sustain within its range [69], the rationale being that an organism will possibly be able to persist in the long-term within areas of lower or similar level of anthropogenic pressure than what it is currently experiencing, with the assumption that the tolerance of humans for its presence will remain similar. This is a conservative approach as refugia could be underestimated for some species that are actually able to sustain higher levels of anthropogenic pressures than what is currently observed. To reflect uncertainty and provide a better decision tool, we recommend testing and reporting variability from using various thresholds. A lower limit on the size of contiguous areas that qualify as refugia for each taxon can also be applied, to meet the requirements for these areas to sustain viable populations [70, but see 71].

In Box 1, we illustrate the Anthropocene refugia concept by mapping realised and potential Anthropocene refugia for two megafauna species, the American bison *Bison bison* and tiger *Panthera tigris*. Both species have undergone massive declines in range and abundance in the past and their persistence is dependent on ongoing conservation programs. Their major ecological roles also make then good candidates for trophic rewilding [72]. While these maps primarily have an illustrative purpose, we briefly discuss potential implications in terms of conservation strategies in Box 1. Details on the methodology to produce these maps are available in the Supplementary Information.

5. Applications in conservation

The concept of Anthropocene refugia fills a gap left open by other conservation approaches that only identify climate change refugia or remnant populations to prioritize conservation efforts. The approach is conceptually similar to that proposed by Allan et al. in a recent study, which combined cumulative human impact with current distributions of terrestrial vertebrates to identify hotspots of impacted species richness

280 and coolspots of unimpacted species richness [19]. However, instead of focusing on species' current range
281 of occurrence, our approach offers a complementary framework in which information from the past is used
282 to understand the potential distribution of a given taxon in the future. We are thus offering a tool to not
283 only define threat mitigation strategies, but to also more fully identify restoration options under future
284 global change and changing anthropogenic pressures. This framework is coherent with the recent
285 designation of 2021–2030 as the "decade of ecosystem restoration" by the United Nations General
286 Assembly and the increasing emphasis put on rewilding as a restoration tool [73]. Identifying those refugia
287 is arguably a challenging exercise and the definition itself is open to further discussion and refinement.
288 With this in mind, we believe there is a high potential for Anthropocene refugia to inform contemporary
289 conservation and restoration, and we suggest possible applications below.

290 ***Realised refugia***

291 Conservation management and restoration within realised Anthropocene refugia is important to maintain
292 existing populations in areas that are predicted to remain suitable for the taxon in the long-term and to
293 promote self-managing, biodiverse ecosystems. This is likely to be facilitated by the lower need for human
294 intervention in areas where taxa are already extant and where the level of anthropogenic pressure is not
295 expected to increase beyond its tolerance level in the near future. This can help identify priority regions for
296 establishing new protected areas, and inform strategies to directly mitigate the threats driving species'
297 declines [19]. It can feed into decision making for conservation management and conservation planning,
298 e.g. following a similar framework as those proposed for climate change refugia [15,16]. This can also be
299 used to identify candidate sites for reinforcements, i.e. the release of an organism into an existing
300 population of conspecifics to enhance population viability [74]. Nonetheless, in a context of fragmented
301 distributions, there is a possibility that populations within these refugia represent sink populations that
302 would become extinct if they are no longer accessible to dispersers [75], or refugee populations confined to
303 suboptimal habitats, with consequences of decreased fitness and density [76]. The viability of populations
304 in these refuge areas could be assessed using information from paleo- and historical ecology as well as field

305 studies [e.g. 77]. Identifying corridors between refugia and maintaining connectivity between these areas is
306 thus important to allow natural dispersal and improve population persistence [4]. These areas can also be
307 affected by ecological imbalances (e.g. from the loss of ecological interactions [78]), causing a need to
308 restore their functionality, e.g. through trophic rewilding [72]. From a socio-ecological perspective, the
309 implications for local populations of focusing conservation actions on these areas should also be considered
310 [79].

311 ***Potential refugia***

312 Mapping potential Anthropocene refugia can form the basis of a more in-depth evaluation of candidate sites
313 for reintroduction and introduction efforts. For many threatened species, conservation success will rely on
314 the expansion of current relict distributions through reintroductions, a strategy that can be guided by the
315 mapping of Anthropocene refugia. By selecting sites that match the biotic and abiotic needs of the focal
316 species in the long-term, this can also inform restoration strategies such as trophic rewilding, an approach
317 promoting self-regulating ecosystems through the introduction of species to restore top-down trophic
318 interactions and associated trophic cascades [72]. It also opens the possibility to change our approach to
319 conservation interventions and translocations to allow the emergence of novel ecosystems that will be robust
320 to future habitat shifts and changing anthropogenic impacts [80]. This may involve planning corridors to allow
321 colonisation through natural dispersal or implementing measures to introduce species outside of their
322 historical range, an approach called assisted colonisation [81].

323 Identifying areas that are most likely to be recolonised in the near future is also important to anticipate the
324 complex impacts this could have on ecosystems as well as interactions with society. The socio-ecological
325 implications of some species' recolonising part of their historical range or occupying new areas should be
326 carefully considered, in particular for species often involved in human-wildlife conflicts, such as large
327 carnivores [82]. Unified socio-ecological approaches that explicitly acknowledge competing perspectives

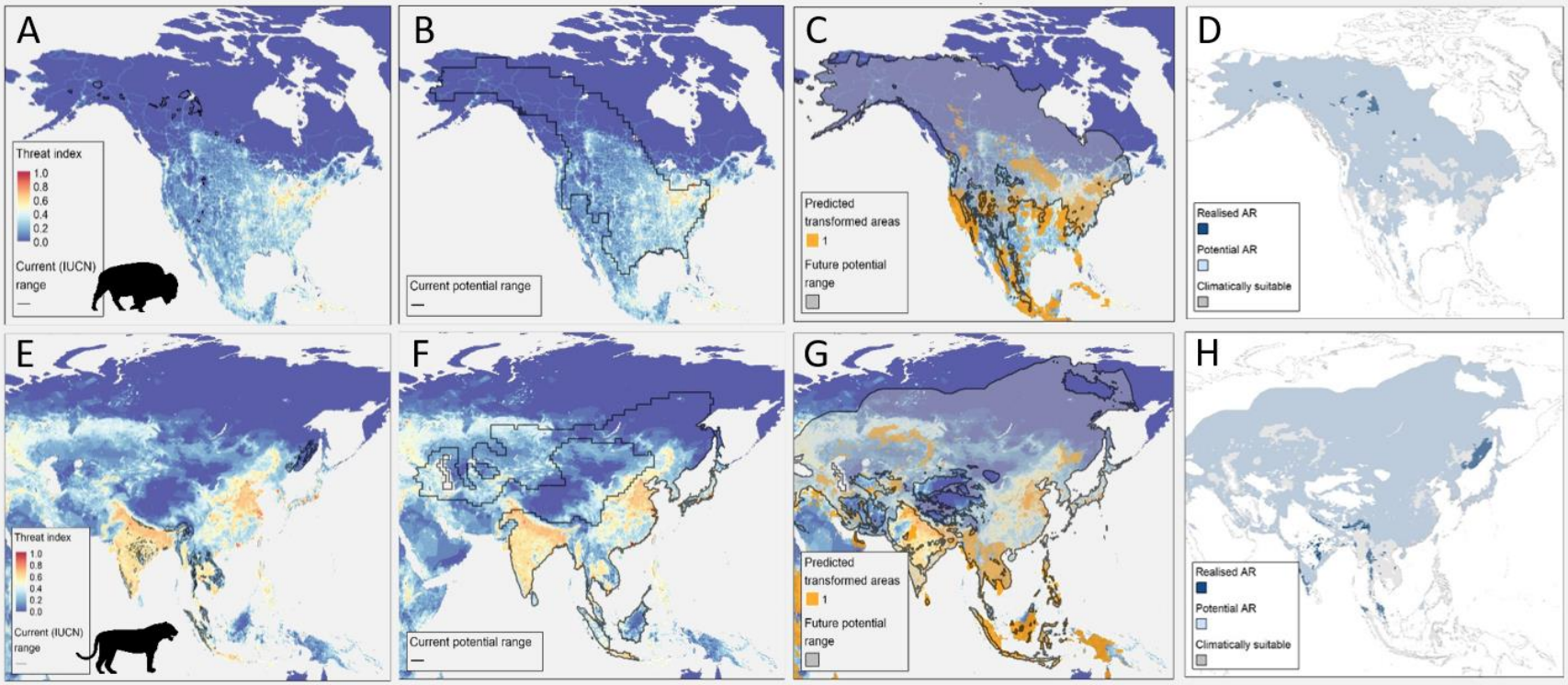
328 between wildlife conservation and social and governance contexts can be applied to provide new insights
329 into management options for sustainable human–wildlife coexistence [83].

330 6. Challenges and opportunities in mapping Anthropocene refugia

331 The highly dynamic state that characterizes the Anthropocene hinders our ability to make predictions for the
332 direction and intensity of changes in the global environment beyond the next few decades. Future global
333 warming, with temperatures predicted to exceed Quaternary levels, will have potential knock-on effects on
334 the entire biosphere and unpredictable consequences for the survival of individual species [84]. This
335 challenges our ability to predict the location of stable Anthropocene refugia, a significant limitation that will
336 not easily be resolved. In this context of uncertainty, focusing conservation efforts on areas that are likely to
337 remain suitable in the near future might be our best option to increase the chances of survival for sensitive
338 taxa and maintain a genetic diversity that will allow future recovery. It also gains time for conservationists
339 and managers to develop long-term solutions for the survival of populations and species. The historical
340 pressures that caused a taxon's local extinction must no longer exist locally for an area to be considered a
341 suitable candidate for restoration. As some threats can be difficult to explicitly include in the mapping
342 exercise, a thorough investigation of past and existing impacts from human activities is necessary before
343 actual conservation recommendations can be proposed. Opportunities to improve the mapping of long-term
344 refugia will increase as we gain a better understanding of taxa distributions' response to climate change and
345 with the future release of spatial data on predicted changes in anthropogenic pressures. As these are
346 integrated into the analysis, one can move from a paradigm focused on places to one focused on dynamics.

347 Another important consideration is the scale at which Anthropocene refugia should be identified and
348 managed. The geopolitical scale used in conservation has an enormous influence on the identification of
349 management areas, with for example low congruence between the network of conservation areas identified
350 at the broad regional *vs* the fine local scale [85]. In practice, the definition of conservation targets is often
351 site-specific. For example, the Natura 2000 network of protected areas, one of the pillars of the European

Community conservation policy, emphasizes the management of specific sites [86]. Finer-scale refugia maps based on local-scale and high-resolution distribution information could thus prove relevant for the identification of land units that will form the basis of management decisions in this context. However, this site-specific approach does not always provide an efficient prioritisation in relation to broader biodiversity concerns [87,88]. Smaller-scale analyses may lead to suboptimal prioritisation with respect to the value for global biodiversity and cost effectiveness, calling for a wider historical and geographical context to contextualise management measures. This demonstrates how conservation strategies can be identified over a wide range of scales and how identifying Anthropocene refugia at both a fine and broad resolution can prove useful for conservation. Ultimately, decisions relative to scale will depend on the objectives of each project and the availability of relevant datasets. The rationale for these choices needs to be explicit and argued, in order to withstand scrutiny and allow for future refinement.



Box 1. Illustration of Anthropocene refugia mapping for the American bison *Bison bison* (A to D) and Tiger *Panthera tigris* (E to H). Maps A-C and E-G are based on the taxa-specific index of current anthropogenic threat, on which we overlaid the areas with a high probability of being converted into cropland or built areas in the future (predicted future transformed areas) for maps C and G. A and E show the current (IUCN) ranges where each species is extant today, B and F show the current potential distributions, and C and G show the potential future range under climate change. D and H show the locations of realised and potential Anthropocene refugia (AR) for the two species, calculated by applying a threshold on the threat index within the potential future range of the species equal to the 95% percentile of the threat level currently experienced by the species. Grey areas are predicted to be climatically suitable for the species in the future but have a value of threat index above the reported threshold. See Supplementary Information for details about the methodology and maps of AR using different thresholds.

American bison. The American bison currently persists in very fragmented and highly managed populations in the United States and Canada. The areas within the northernmost part of the range, which are within the future predicted range for the species and with low levels of threats now and in the future, are realised refugia for the species. Conservation actions could focus on managing and reinforcing populations in these areas, e.g. by enforcing protection and building corridors between these populations. The climatically suitable area is also predicted to expand in Canada and Alaska under future climate change, and land in these areas is not predicted to be transformed in the near future, making these regions potential refugia. These are good candidate areas to restore bison populations through reintroductions or assisted colonisation. On the contrary, the southern part of the current potential range has a high level of threats and the range of the species is predicted to contract and fragment under future climate change. Conservation and restoration in this area will thus require greater efforts.

Tiger. The current range of the tiger is very fragmented and located in areas surrounded with high anthropogenic pressures (e.g. in India). Some of these areas represent realised refugia because they are predicted to remain within the range of the species under future climate change and the anthropogenic pressures are not expected to increase (e.g. protected areas in India, Bhutan, China and southeast Asia and in the Russian Far East). Threat levels in northeast China, Russia, Mongolia and Kazakhstan are low and the climate suitability is predicted to remain stable. These are potential candidate areas for restoration, although a more thorough investigation of historical threats that drove the species' local extinction in these areas would be needed to shed light on their current suitability. Other areas are part of the current potential range of the species, but may become unsuitable in the future because of predicted range shifts under climate change (e.g. Borneo) or a predicted increase in land-conversion (Southeast Asia and part of Indonesia). These elements could be taken into account for establishing conservation priorities to ensure the species' long-term persistence.

363

7. Conclusion

We here introduce a novel concept – Anthropocene refugia – to account for the role of anthropogenic pressures in defining realised and potential refugia for biodiversity in a human-dominated planet. Our main intention is to call for a better consideration of the full range of anthropogenic pressures, beyond climate change, to identify refugia in the Anthropocene, while at the same time assessing re-expansion possibilities. We also emphasise the importance of considering a long-term perspective in defining a taxon's potential distribution, to overcome the shifting baseline syndrome that affects our understanding of natural biogeographical patterns, limiting many assessments of restoration options. We highlight key possible applications of the concept with special emphasis on its potential to inform restoration approaches such as trophic rewilding, as well as nature management more generally, in the face of contemporary climate change. It is our hope to see a larger range of potential applications of this approach discussed and implemented in the future. Despite the many challenges, we argue that the Anthropocene refugia concept has the potential to bridge important gaps in our perspectives on the past (the distribution and ecology of wildlife prior to severe human pressure), present (where wildlife occur now in a human-dominated world) and future (where society could hopefully allow wildlife to exist in a reconciling world), thus representing both an important concept to reflect on our coexistence with wildlife on this planet, and an integral component of the conservation and restoration toolbox to protect and promote biodiversity in the Anthropocene.

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