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1 **Assessing species vulnerability to climate change**

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60 **Abstract**

61 The effects of climate change on biodiversity are increasingly well documented, and many
62 methods have been developed to assess species' vulnerability to climatic changes, both ongoing and
63 projected in the coming decades. To minimize global biodiversity losses, conservationists need to
64 identify those species that are likely to be most vulnerable to the impacts of climate change. In this
65 review, we summarise different currencies used for assessing species' climate change vulnerability.
66 We describe three main approaches used to derive these currencies (correlative, mechanistic and
67 trait-based), and their associated data requirements, spatial and temporal scales of application and
68 modelling methods. We identify strengths and weaknesses of the approaches and highlight the
69 sources of uncertainty inherent in each approach that limit projection reliability. Finally, we provide
70 guidance for conservation practitioners in selecting the most appropriate approach(es) for their
71 planning needs and highlight priority areas for further assessments.

72

73 The Earth has warmed by about 0.74 °C in the last 100 years, and global mean temperatures
74 are projected to increase further by 4.3 +/- 0.7 °C by 2100¹. Agricultural expansion,
75 overexploitation and invasive alien species introductions have been the main drivers of biodiversity
76 loss in the recent past, but several lines of research suggest that climate change could become a
77 prominent, if not leading cause of extinction over the coming century², both via direct impacts on
78 species and through synergies with other extinction drivers^{1,3}. Species have already responded to
79 recent climatic shifts⁴⁻⁸, and various attempts have been made to assess the potential risks to
80 biodiversity posed by climate change over coming decades⁹⁻¹¹.

81 To assess the threats to a species posed by climate change one must have information
82 regarding its vulnerability, which is defined by the IPCC as ‘the predisposition to be adversely
83 affected’¹². Although there is currently no broad consensus in the scientific literature regarding the
84 definition of ‘species’ vulnerability’, it is generally accepted that this is a function of both intrinsic
85 and extrinsic factors¹³, and assessments often consider exposure, sensitivity and adaptability in
86 combination^{13,14}. Exposure is the magnitude of climatic variation in the areas occupied by the
87 species¹⁵. Sensitivity, which is determined by traits that are intrinsic to species, is the ability to
88 tolerate climatic variations, while adaptability is the inherent capacity of species to adjust to those
89 changes^{14,15}. Attempts at projecting the effects of climate change on species have used both
90 different currencies (i.e. the range of measures used to assess species’ climate change vulnerability)
91 and divergent approaches for identifying the most vulnerable taxa. Because of this lack of
92 consensus by the conservation community, a formal comparative evaluation is necessary to guide
93 sensible choices of the most appropriate technique(s) for assessing species’ vulnerability.

94 Here we provide the first comprehensive review of currencies and approaches that have been
95 used to assess species’ vulnerability to climate change, based on a total of 97 studies published
96 between 1996 and 2014 (with >70% of the studies published during the last five years). We
97 describe the four dominant currencies of species’ climate change vulnerability assessments and

98 provide examples of how these have been applied. Three broad categories of approaches plus three
99 combinations thereof were identified, and we describe each examining how they address
100 uncertainties, and discuss their key limitations. Finally, we provide guidance for practitioners. Via
101 these analyses, we aim to help conservationists select appropriate approaches for assessing species'
102 vulnerability, such that climate change adaptation responses are as solidly based as possible.

103

104 **Taxonomic and regional application of climate change vulnerability assessments of species**

105 We conducted a systematic literature search using ISI Web of Knowledge. Key-words were
106 selected to identify studies on climate change (climate change*, global warming*, sea-level rise*,
107 elevated CO₂*, drought*, cyclones*, CO₂ concentration*) impacts (population reduction*, range
108 changes*, range shift*, turnover*, extinction risk*, extinction probability*) that led to vulnerability
109 assessments (vulnerability*, sensitivity*, adaptability*, exposure*) based on different types of
110 approaches (mechanistic*, SDM*, correlative*, trait-based*, criteria*, niche models*). We then
111 selected the most representative papers (in terms of both spatial and temporal scales, and taxa).
112 Studies differed widely in taxonomic coverage, birds being the most frequently considered taxon,
113 followed by mammals and plants, while non-insect invertebrates being seldom assessed (Fig. 1).
114 Additionally, spatial scales of application and authors' interpretations of the concept of
115 vulnerability varied extensively. More than 60% of the studies were developed at local scale, while
116 only 4% of the papers assessed species' vulnerability globally (Fig. 1). As a result, numerous
117 species have been assessed in only part of their range and their estimates of vulnerability may
118 therefore be unrealistic.

119 Many published studies have shown that life-history traits are more important than
120 taxonomy and distribution in determining species vulnerability to climate change¹⁴. Traits that
121 commonly make a species vulnerable to climate change include limited dispersal abilities^{14,16-18},

122 slow reproductive rates^{11,19}, specialised habitat and dietary requirements^{14,20,21}, restricted
123 distribution and rarity^{14,22}, and narrow physiological tolerances^{23–25}, while potentially vulnerable
124 habitats include intertidal areas, montane habitats, savannahs and grasslands²⁵. Knowing what
125 makes a species vulnerable and where vulnerable species are located can be very useful when
126 practitioners need to assess the vulnerability of species for which only basic knowledge of their
127 biology and ecology is available.

128 Studies conducted at a broad scale (regional, continental and global, almost 70% of the
129 total), were used to derive a map of the areas with the greatest concentration of vulnerable species,
130 according to an ecoregional classification (Fig. 2). For marine areas we performed a qualitative
131 assessment (high, medium and low vulnerability, mostly based on Foden *et al.*¹⁴) because only a
132 few marine taxa have been evaluated at broad scales and more than 80% of the species assessed are
133 corals, while for terrestrial areas we were able to identify hotspots of vulnerable species as areas
134 with high concentrations of vulnerable species (> 100), belonging to different taxonomic classes.
135 These vulnerable areas, the Caribbean, the Amazon basin, Mesoamerica, eastern Europe through
136 central and eastern Asia, the Mediterranean basin, the Himalayas, South-East Asia, North Africa,
137 the Congo basin, tropical West Africa and Madagascar, should be a first priority for monitoring.
138 However, over 70% of the studies we reviewed involved only three continents/subcontinents, with
139 almost 33% of the studies in North America, 24% in Europe, and 14% in Australia (Fig. 3). By
140 contrast, there is a paucity of studies in the most biodiverse tropical and subtropical regions of the
141 world. Since climate change will act in concert with other threats, and habitat loss is predicted to
142 severely affect biodiversity in developing countries²⁶, it is essential to conduct studies in these data
143 deficient areas.

144

145 **Currencies used to assess vulnerability: ‘WHAT’**

146 There is no standard way to assess a species’ vulnerability to climate change, and the type of
147 information (e.g. range extent, population size) needed will determine which approaches are most
148 appropriate.

149

150 **Distributional changes**

151 To assess climate change impacts on species, current and future distributions can be
152 projected using either mechanistic or correlative niche models (both approaches are discussed
153 below), which relate environmental conditions to species’ physiological responses or occurrence
154 data, respectively. Several analyses have provided examples of species likely to suffer range
155 reductions in the 21st century^{16,18}. For example, Vieilleident *et al.*²⁷ predicted that the Malagasy
156 baobab *Adansonia suarezensis* is likely to go extinct before 2080 due to an overall loss in suitable
157 habitat. Changes in range size have usually been assessed by considering the climatic characteristics
158 of current distributions and the projected distribution of these climatic conditions in future^{27,28}.
159 However, vulnerability might be exacerbated by other factors, including biotic interactions, reduced
160 adaptive evolutionary response and dispersal ability. Several studies have incorporated dispersal
161 ability into predictions of future range changes, either by contrasting scenarios of no dispersal with
162 unlimited dispersal^{29–31}, by estimating average or maximum potential dispersal distances^{16,18,24}, or
163 by explicitly simulating metapopulation dynamics including dispersal events^{32,33}. For example,
164 Schloss *et al.*¹⁸ suggested that 87% of Western Hemisphere terrestrial mammals will likely
165 experience a reduction in their climatically suitable area, with 20% of these species being
166 particularly vulnerable due to their limited dispersal ability.

167

168

169 **Population changes**

170 A different set of modelling approaches uses predictions of population trends to inform risk
171 assessments³⁴. Quantified population changes can be based on direct observations, indices of
172 abundance^{34–36}, reporting rates used as proxies for abundance³⁷, or they can be inferred from
173 declines in extent of occupied or suitable habitat^{34,38}. Examples of observed population declines
174 within recent decades include long-distance avian migrants to Dutch forests, which have likely been
175 driven principally by temperature changes in spring³⁵. Also, a decrease in ice coverage has led to a
176 reduction in polar bear (*Ursus maritimus*) numbers in the southern Beaufort Sea³⁹. Some
177 approaches to projecting future population sizes incorporate past population trends into mechanistic
178 models^{39–41}, and consider the effects of changes in model parameters (e.g. distribution patterns, life
179 history, climatic conditions). This type of approach has also been applied to a population of
180 American marten (*Martes americana*) in North America, where explicit population models have
181 been used to simulate a 40% decline in the population due to climate change by 2055⁴².

182

183 **Extinction probability**

184 One synthesis estimated that between roughly 20 and 30% of species assessed are likely to
185 be at increasingly high risk of extinction in the face of increasing global warming¹². Extinction
186 probability has been calculated for populations of species with known life-history characteristics,
187 like the emperor penguin (*Aptenodytes forsteri*)⁴¹, Arizona cliffrose (*Purshia subintegra*)⁴³, spring-
188 summer chinook salmon (*Oncorhynchus tshawytscha*)⁴⁴ and polar bear (*Ursus maritimus*)³⁹, by
189 using Population Viability Analyses^{41,43}, demographic models^{39,44,45}, or evolutionary models⁴⁶.
190 These methodologies combine population fluctuations with changing environmental parameters in
191 order to estimate extinction probability within a given time interval. For example, Fordham *et al.*⁴⁵
192 modelled the predicted abundance of the Iberian lynx (*Lynx pardinus*) under three climate scenarios

193 by integrating temperature and precipitation data, prey availability and management interventions,
194 and predicted that climate change may drive this species to extinction within the next 50 years. This
195 work relied upon a thorough understanding of the species' biology and of demographic dynamics
196 related to extinction risk. However, as most species lack such detailed data, extinction risk due to
197 climate change tends to be quantified only for better-known species.

198

199 **Vulnerability indices and other relative scoring systems**

200 Vulnerability indices are quantitative indicators of the relative vulnerability of species. The
201 data derived from the currencies discussed above, and from trait-based vulnerability assessments
202 (TVAs), can be used to obtain scores¹⁴, categories³⁴ or indices⁴⁷, which are often easier for scientists
203 and practitioners to interpret and use, in order to identify species at risk within their focal areas.
204 Foden *et al.*¹⁴, for example, classified birds, amphibians and corals into two vulnerability categories
205 (low or high). One limitation of indices and scores is that they do not provide any direct measures
206 of the expected impact on species, i.e. they are not expressed in terms of any of the currencies
207 otherwise used to assess species' vulnerability (e.g. range reductions, extinction probability,
208 population decline).

209

210 **Approaches used to model species' vulnerability to climate change: 'HOW'**

211 Different approaches are used to assess species' vulnerability to climate change. These
212 approaches can be placed in four classes: 1) correlative, 2) mechanistic, 3) trait-based, and 4)
213 combined approaches.

214

215

216 **Correlative approaches**

217 Distributional changes are typically estimated through the use of correlative models that aim
218 to represent the realized niche of a species^{48,49}. Correlative models relate observed geographic
219 distribution of a species to current climate; resultant models are then applied to climate projections
220 to infer potential climatically-suitable areas for a given species in the future. Species' distribution
221 can be presence-only data^{17,22}, presence/absence⁵⁰ or abundance observations⁵¹, based either on
222 fieldwork or specimen records^{22,52}. Correlative models have been applied to species at scales
223 ranging from local to global^{19,53} (Fig. 1), and have been widely used to explore the vulnerability of
224 vertebrates (including birds^{36,52,54}, mammals^{17,28}, amphibians^{30,50}, fishes^{22,55}), invertebrates^{14,56,57}
225 and plants^{27,58}.

226 Correlative models have the advantage of being spatially explicit and they are applicable to
227 a wide range of taxa at various spatial scales. However, there are a number of limitations and
228 uncertainties associated with them (see Pearson *et al.*²⁹ and Wiens *et al.*⁵⁹ for detailed descriptions).
229 Primary sources of uncertainty and potential errors can be divided into three broad classes: climatic,
230 algorithmic, and biotic^{29,59}. Climatic uncertainties, that apply to all types of approaches, may arise
231 from general circulation models, which use different parameters and model structures to simulate
232 future climate systems, and may produce different results irrespective of the assumed greenhouse
233 gas emissions^{59,60}. Climate models project future climate conditions at a coarser scale of resolution
234 than that of data (biological and environmental) used to calibrate the correlative models^{49,59}, and
235 their outputs are thus often not sufficiently fine-scaled for modelling rare species or species with
236 small geographic distributions^{49,50}. Algorithmic uncertainties can arise from the differences in
237 methods and models used to predict species' distribution (e.g. Generalized Additive Models,
238 Maximum Entropy models), and from the selection of model predictors (e.g. mean annual
239 temperature, annual precipitation; see⁶¹), which have shown great variability in both results and
240 model performance. This range of uncertainties has been addressed by some by applying a variety

241 of different statistical methods and model structures, summarising predictions across all models to
242 generate ensemble forecasts, e.g. model-averaged probability of presence and confidence intervals
243 (see examples^{16,30,62}). Biotic uncertainties may arise if the assumptions made about a species'
244 biology are inappropriate. First, species' distributions are assumed to be in equilibrium with
245 surrounding climates and these relationships are assumed to persist in the future⁵⁶. Second, it is
246 unknown how much of a species' fundamental niche, exclusively determined by the species'
247 requirements and/or tolerances is represented by its currently realized niche, which is also
248 determined by abiotic, biotic, geographic, historical and anthropogenic factors⁴⁹. Moreover,
249 correlative models for plants do not account for drivers such as changes in atmospheric CO₂
250 concentration, which influence plant growth and water use and can alter demographic processes
251 sufficiently to drive ecosystem structural and functional changes⁶³. Correlative models can also be
252 used to predict future geographic distribution of a group of species in a given area and the results
253 combined to create assessments of new community structures⁶⁴. However, these models ignore
254 community-assembly rules, as well as differences in the constraints and adaptability of individual
255 species, and thus the resulting predicted species assemblages may be unrealistic⁶². Correlative
256 models have been criticised by some authors because they lack mechanism and causality (e.g.
257 see⁶⁵), although there is increasing evidence that recent population trends have matched those
258 expected from correlative model projections³⁶.

259 The relatively large number of reliable occurrence points required to fit correlative models
260 often precludes their use for assessments of poorly known species⁶⁶. They are also less appropriate
261 for species with cosmopolitan or limited geographic distributions (e.g. on small islands) since
262 climate may not explain distributions or distributional changes. Despite these limitations, the
263 majority of regional and global analyses to date are based on correlative approaches, since they can
264 be relatively quick and cheap to apply⁶⁷ and occurrence data are available for a large number of
265 taxa.

266 **Mechanistic approaches**

267 Mechanistic models require taxon-specific parameters that provide information on the
268 behaviour of individuals and the mechanisms they develop to cope with changing climatic
269 conditions. Mechanistic models are developed from laboratory and field observations of
270 demographic rates, physiological tolerances^{41,68,69}, competition and dispersal⁷⁰, diseases and
271 predation⁷¹, as well as from energy balance equations⁷². Measures of vulnerability derived from
272 these models are typically expressed in terms of probability of extinction, whether of discrete
273 populations or entire species. Mechanistic approaches often focus on a single species of
274 conservation interest (e.g. rare or threatened species)^{39,41}, since methods used to collect detailed data
275 on species physiology, which are essential to parameterise such models, are costly and time-
276 consuming. Some studies exist involving this type of modelling that do not involve a specific taxon
277 but rather provide general theoretical frameworks to predict effects of climate change on plants¹⁰,
278 terrestrial ectotherms⁶⁸ and generic species^{9,10}, highlighting major determinants of extinction risk in
279 a changing environment and providing recommendations for future research needs. Some
280 mechanistic models (e.g. incidence function models, age-structured metapopulation models) may be
281 used to explain metapopulation dynamics in the presence of climate change by estimating extinction
282 and colonization rates as functions of habitat suitability⁷³, prey availability or management
283 actions⁴⁵. Other mechanistic models consider the changes in vegetation distribution and dynamics
284 using both bioclimatic and physiological parameters of groups of species (e.g. plant functional
285 types)⁷⁴.

286 Mechanistic niche models utilise species' functional traits, physiological tolerances and
287 energy and mass exchanges to represent the fundamental niche of a species⁷⁵. Key functional traits
288 (e.g. morphology, physiology, behaviour) and spatial habitat data (e.g. climate, vegetation cover,
289 topography, bathymetry) are used to assess individual fitness^{75,76}. Such models are considered by
290 some authors to be more robust and theoretically defensible than correlative models for predicting

291 species' responses to climate change⁷⁵. Compared to the realized niche modelled via correlative
292 approaches, the mechanistically modelled fundamental niche provides a better approximation of the
293 climatic space in which an organism can exist, including areas that have, or may, become newly
294 suitable^{75,76}. In addition, these models permit explicit consideration of important biological factors
295 like evolutionary changes and physiological responses.

296 Extensive application of mechanistic niche models is precluded by the fact that they require
297 detailed data that are lacking for most species. The main sources of uncertainty in mechanistic
298 models relate to model parameters (e.g. population abundance, which may be underestimated
299 depending on the method used to collect the data and the ability of the observer to detect the
300 species), and to combining data collected at different spatial resolutions²³. Moreover, these models
301 usually do not account for non-climatic threats to dispersal or for biotic interactions⁴⁸.

302

303 **Trait-based vulnerability assessment approaches**

304 TVAs use species' biological characteristics as predictors of extinction risk due to climate
305 change^{13,14}, often in combination with estimates of exposure. Methods typically involve selecting
306 traits related to sensitivity (e.g. typically describing ecological specialization, inter-specific
307 interactions) and adaptability (i.e. dispersal and phenotypic adaptability^{14,77,78}) and scoring each
308 according to observations or expert judgment^{79,80}. For example, Gardali *et al.*⁷⁸ quantified the
309 vulnerability of Californian birds by scoring sensitivity and exposure for each taxon. They used
310 information from published literature to assign a sensitivity score to four intrinsic species'
311 characteristics (dispersal ability, migratory status, habitat specialization and physiological
312 tolerances), and then combined sensitivity and exposure scores to generate a climate vulnerability
313 index.

314 TVAs are being used increasingly by conservation organizations and management agencies
315 because they permit a relatively rapid assessment for multiple species, which can be used to
316 prioritize conservation planning and implementation of adaptation schemes. Moreover, TVAs are
317 sometimes considered easier to use by practitioners because they do not require extensive
318 knowledge of modelling techniques, even if their applicability is limited to a specific area and to
319 cases where relevant data on species' traits are available (see⁸¹).

320 Drawbacks with TVAs are that precise vulnerability thresholds associated with each trait are
321 often unknown, necessitating selection of arbitrary, relative thresholds for categories of higher or
322 lower extinction risk. Traits are often weighted equally²⁰ even though some characteristics are likely
323 to be more important than others in determining climate change vulnerability. Subject to the
324 challenges of score-based systems, it is not possible to compare vulnerability between taxonomic
325 groups for which different sets of traits may have been used in the TVA. Moreover, different TVAs
326 applied to the same species do not always yield congruent results⁸². The most common sources of
327 uncertainty in TVAs stem from the choice of traits included in assessments, parameterisation of
328 thresholds of associated vulnerability, and from gaps in knowledge of individual species'
329 characteristics^{14,83}. For example, dispersal distance is one of TVA's most important and
330 conservation-informative traits, yet estimates are currently available for few animal species. Some
331 studies have attempted to provide dispersal estimates^{16,18,84}, but inevitable uncertainties arise from
332 models and parameters. Uncertainty is usually incorporated as a confidence score based on expert
333 opinion. Such score can be provided for each trait⁷⁸, for each stage of the assessment⁸³, or for the
334 overall assessment⁷⁸. Alternatively, some authors rank missing trait data under best- or worst-case
335 scenarios^{14,80}, by assuming optimistic and pessimistic extreme values.

336

337 **Combined approaches**

338 There is a growing consensus on the benefits of using approaches that combine different
339 types of models and data^{32,40}. Here we discuss the three most common combined approaches,
340 criteria-based, mechanistic-correlative and correlative-TVA.

341

342 **Criteria-based approaches**

343 Criteria-based approaches have been used to combine observed or projected demographic
344 trends (e.g. population increases or decreases) with intrinsic characteristics of species (e.g.
345 generation length), to classify species into threat categories based on the risks posed by climate
346 change. Climate-attributed changes in species' geographic ranges, often derived from correlative
347 models, are assessed against quantitative thresholds^{34,38,83,85}. These assessments often use the IUCN
348 Red List categories and criteria (www.iucnredlist.org)^{38,85} or draw inspiration from them⁸³.

349 One advantage of criteria-based approaches is that they can be applied to large numbers of
350 species worldwide⁸⁶. They are important for assessing the conservation status of species threatened
351 by climate change since they simultaneously account for several factors known to affect the relative
352 extinction risk (e.g. declines in the extent of occurrence, reduction in population size). Furthermore,
353 by using quantitative thresholds to predict relative extinction risk, it is possible to make
354 comparisons between past, current and future conservation status of species. Approaches based on
355 the IUCN Red List require a consistent adoption of thresholds and criteria⁸⁷; however, these are
356 sometimes arbitrarily modified (e.g. to temporal and spatial scales and spatial resolution), thereby
357 reducing the comparability and interpretability of the results⁸⁷. Pearson *et al.*⁸⁸ identified factors that
358 predispose a selection of North American herpetiles to high extinction risk due to climate change,
359 and concluded that most important factors are already incorporated into extinction risk assessments
360 for the IUCN Red List.

361 **Mechanistic-correlative and mechanistic-correlative-TVA approaches.**

362 In mechanistic-correlative approaches, outputs of correlative models are incorporated into
363 demographic models to calculate spatial structure of populations⁴⁵, whose dynamics are then
364 modelled mechanistically. This combination is useful, for example, in predicting how distribution
365 patterns influence the viability of populations under a changing climate^{32,40}. Furthermore, some
366 studies have integrated life-history characteristics into models to produce more accurate projections
367 of species' responses to climate change. Keith *et al.*³² assessed extinction risk for plant species in
368 South African fynbos under stable and changing climatic conditions. The authors linked the outputs
369 of correlative models with a demographic metapopulation model, and considered their interactions
370 with fire tolerances and dispersal abilities. In this way, they dealt with both habitat changes and
371 population dynamics simultaneously in their assessments.

372

373 **Correlative-TVA approaches**

374 Other combined approaches integrate species characteristics and species distribution models
375 by incorporating species traits to refine distribution projections made using correlative
376 models^{16,18,31,89}, or by integrating correlative model outputs into trait-based assessments^{21,83}. In the
377 first approach, traits like dispersal ability and generation length have been usefully applied to refine
378 range dynamics^{16,90}. For example, Barbet-Massin *et al.*¹⁶ used natal dispersal and generation length
379 to predict the breeding distribution of European birds under climate and land-use changes. The
380 authors predicted a 10% reduction of future species richness assuming unlimited dispersal and a
381 25% reduction by using natal dispersal.

382 In the second type of approach, the outputs of correlative models are used to estimate
383 exposure to climate change and identify areas, which might become suitable in the future, even if
384 they fall outside a species' current range. By linking exposure, estimated with correlative models,

385 with sensitivity and adaptability assessed with TVAs, a vulnerability index can be calculated that
386 accounts for both intrinsic and extrinsic factors (e.g.⁸³).

387

388 **Guidance for selecting climate change vulnerability assessment approaches**

389 Ideally, practitioners should assess the vulnerability of populations or species to climate
390 change using a variety of methods, with greatest predictive confidence conferred where models are
391 in agreement. The choice of the approach is entirely dependent on conservation goals, which are
392 often vague and not clearly defined, and on the data available (Box 1). Relying on these broad
393 goals, practitioners need to identify definable and measurable objectives⁹¹, in terms of temporal,
394 spatial and taxonomic scales. In Table 1 we identify different examples of objectives against each
395 approach and below provide two exemplary goals and identify the associated methodologies to
396 reach them.

397

398 **Estimating extinction risk**

399 When deriving estimates of extinction risk of species is the goal, both mechanistic and
400 correlative models can provide appropriate results. The most effective way to predict extinction risk
401 of species under climate change is to combine demographic data (e.g. population trends, survival,
402 fertility) with changing environmental factors (e.g. precipitation, sea ice extent), and then project
403 these changes into the future^{41,43}. For example, Jenouvrier *et al.*⁴¹ used a mechanistic model, which
404 combined demographic and climatic data, to project a > 35% probability of extinction for the
405 emperor penguins (*Aptenodytes forsteri*) in Antarctica by 2100 in response to projected sea ice
406 changes.

407 Another way of inferring the extinction risk of species is to use a decline in suitable area as a
408 proxy for population decline^{38,92,93}, providing the relationship between the two can be assumed to
409 remain constant. Correlative models can be used to project range changes into the future; this would

410 allow classifying the species into one of IUCN Red List categories. Levinsky *et al.*⁹³, for example,
411 demonstrated that the proportion of European mammals that are forecast to become extinct by 2100
412 can vary from 1 to 9%, depending on the magnitude of predicted climatic changes and the ability of
413 species to migrate.

414

415 **Prioritization of actions**

416 Climate change adaptation strategies require creating a link between an explicitly stated
417 expectation about the way global warming could affect species, habitats, or even people, to clear
418 objectives and actions that would best address those climate impacts⁹⁴. Conservation decision-
419 making is about prioritizing actions to satisfy conservation objectives for a set of species and
420 areas⁹⁵. It is not possible to make conservation interventions for all species, and prioritization
421 exercises are needed to determine which actions to focus on to protect species⁹⁶. Given the high
422 levels of uncertainty and complexity in modelling impacts, we highlight that reprioritizing or even
423 abandoning actions which benefit some species over others should be done with great caution.

424 Where site-scale conservation is the focus (e.g. in a protected area), correlative models are
425 able to identify species for which the area may be suitable in the future, thereby allowing managers
426 to prepare for potentially novel species assemblages and plan appropriate conservation actions (e.g.
427 predator and invasive species control). For example, Hole *et al.*⁵⁴ used correlative models to assess
428 species turnover in a network of Important Bird Areas in Africa, and provided generic guidance on
429 the types of conservation actions (e.g. translocation, habitat restoration, disturbance-regime
430 management) that might be most appropriate for individual sites.

431 For a regional-scale focus, identifying the bioclimatic space where species could persist and
432 the areas of relatively unchanged climate within this space may facilitate species persistence during
433 periods of climatic stress. Spatially explicit projections from correlative and mechanistic niche
434 models allow identification of these sites. For example, Maschinski *et al.*⁴³ used a mechanistic

435 approach to identify potential climatic refugia for an endemic plant species (*Purshia subintegra*) of
436 Arizona. This study showed that in situ manipulation and introductions at northern latitudes are
437 priority actions necessary to prevent the extinction of this rare and endangered species.

438 Where the focus is on particular species, trait-based and mechanistic approaches are likely to
439 deliver insights into the specific mechanism(s) of impact (e.g. increased competition, loss of
440 mutualisms, disruption of cues, disease)¹⁴, allowing targeted interventions both to decrease species'
441 sensitivity (e.g. disease treatment, predator control) and to increase their adaptive capacity (e.g.
442 genetic management, improved landscape permeability, translocation)⁷⁵. Indices calculated with
443 trait-based approaches can facilitate grouping taxa by their relative risk to climatic changes, which
444 help identify adaptation strategies that could benefit multiple species⁷⁷. For example, Moyle *et. al*⁸⁰,
445 who assessed Californian freshwater fishes according to their life-history characteristics, classified
446 species that were heavily dependent on human intervention as highly vulnerable to climate change,
447 and highlighted the need for conservation actions such as management of barriers, special flows and
448 removal of alien species to allow population persistence.

449

450 **Conclusions**

451 This review of climate change vulnerability assessment approaches suggests that, in general,
452 a correlative approach is appropriate when the only data available are those on species' occurrence,
453 in particular for reconstructing the paleoclimatic niche of fossil species or projecting their future
454 climatic suitable area, from local to global scales. On the other hand, mechanistic models have the
455 greatest power to assess extinction probability driven by climate change, identify conservation
456 actions and evaluate the potential effectiveness of management interventions, but they are limited to
457 few terrestrial species. Therefore, they are usually employed when the focus is on a well-studied
458 species of particular conservation interest (e.g. species threatened, keystone, flagship or umbrella),
459 for which detailed physiologic and/or demographic data are available. Trait-based approaches are

460 less resource-intensive and therefore more widely used. This method is ideal to help non-GIS
461 experts develop regional assessments and to identify conservation priorities in the absence of
462 specific data on species' distribution.

463 Validation of the accuracy and precision of vulnerability assessment approaches, through
464 comparison of model projections with a globally coordinated observation effort, is essential for
465 improving projections of the impacts of climate change on species. Use of paleoecological evidence
466 of past species' responses to climatic variation in conjunction with matching paleoclimatic data can
467 provide an opportunity to test the assessments^{97,98}. Observations of recent responses to climate
468 change are another useful tool to test reliability of model predictions against current observations.
469 However, quantifying the ability of models to provide reliable range shift projections or population
470 changes is still challenging, since they are often difficult to validate across time and space⁹⁷. One
471 key issue is the debate on modelling the realized vs. the fundamental niche^{48,49,79}. Both the lack of
472 equilibrium between species and climate, and the difficulty of isolating the effects of climatic
473 changes on a species' range from those of other threats⁹⁷, can lead to changes in the realized niche
474 of a species (usually modelled mechanistically). On the other hand, correlative approaches attempt
475 to model the fundamental niche of a species, but they use data from the realized niche⁴⁸. This can
476 lead to spurious correlations between species' occurrence and climate and thus hinder model
477 validation as well as casting doubts on model accuracy⁴⁸. For example, a species may not respond to
478 climate only because other factors (e.g. competitive exclusion, predation) are confounding the
479 response⁹⁹. Additionally, when comparing past and current distribution to validate models or TVAs,
480 a big challenge is to find accurate information on species' historic distribution and population
481 trends. Addressing all of these issues should lead to better conservation decision-making.

482 A glaring oversight in almost all studies is that they only focused on the direct impacts of
483 climate change. Indirect impacts within biological communities, as well as changes in human use of
484 natural resources are going to have substantial, complex, and often multiplicative impacts on

485 species^{36,100}. Thus, many current assessments are blind to the fact that the interactions between
486 current threats and climate change are likely to be profound³. Moreover, the growing human
487 population will itself be increasingly affected by climate change, with human adaptation responses
488 likely to result in substantial and negative impacts on biodiversity¹⁰⁰. Assessments of future impacts
489 of climate change need to take these factors into account.

490

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728 **Author contributions**

729 M.P., P.V., C.R., J.E.M.W. and W.B.F. designed the framework for the review. All authors contributed to the
730 writing, discussed the results and commented on the manuscript.

731

732 **Competing financial interests**

733 The authors declare no competing financial interests.

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735 **Figure headings:**

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737 **Figure 1:** Taxonomic focus of vulnerability assessments in the analysed papers.

738 Birds are the most analysed taxon, followed by mammals and plants, while invertebrates other than
739 insects have seldom been assessed. Colours represent the spatial scale of the assessments. Regional
740 scale is defined as describing the range of 10^4 to 10^7 km², while scales smaller than 10^4 km² are
741 referred to as local scales.

742 **Figure 2:** Ecoregional global concentrations of terrestrial and marine climate change vulnerable
743 species.

744 Studies conducted at regional, continental and global scales were used to derive a global map of
745 vulnerability, according to an ecoregional classification. The red scale represents terrestrial areas
746 with high numbers of vulnerable species, identified on the basis of 1) the number of species
747 assessed and 2) the taxonomic ranks higher than species considered. The blue scale represents areas
748 that host marine vulnerable species. Dark colours indicate areas of high vulnerability, while light
749 colours indicate areas of relatively low vulnerability.

750 **Figure 3:** Trends and biases in taxonomic groups assessed and approaches used by continent.

751 Birds and mammals have been the most frequently analysed taxa across all continents between 1995
752 and 2014, usually with similar proportions (with the exception of Asia). Correlative approaches are
753 widely used for assessing species vulnerability in Africa, Asia and Europe, while mechanistic
754 approaches prevail in North America. Trait-based approaches are used mostly in Australia and
755 North America.

756

Table 1 | Examples of objectives in climate change vulnerability assessments, on the basis of the scale to be adopted.

	Temporal scale			Spatial scale			Taxonomic scale		
	Past	Recent past/ present	Present/ Future	Local/site	Regional	Global	Population and ranks < than species	Single species	Multispecies
Examples of objectives: correlative	Reconstructing species' past distribution ¹⁰¹	Modelling current climatic suitable areas for species ²²	Predicting climate-induced future range shifts under different time intervals ¹⁰²	Quantifying the area that will remain climatically suitable for species living in areas important for conservation ⁶⁰	Assessing the ability of a network of protected areas to ensure the persistence of species ¹⁰³	Identifying the most important climatic variables in determining a species' distribution globally ¹⁹	Quantify the latitudinal/ altitudinal shifts of the various populations of a species ¹⁰⁴	Assessing a species' future threat status ⁹³	Predicting spatial patterns of species richness ¹⁰⁵
	Identifying past climatic refugia ¹⁰⁶	Quantifying % range gains/losses in the last decades to estimate extinction risk ³⁸	Projecting future range margin contractions/expansions by 2080 ⁹²	Quantifying species' turnover within a protected area ⁵⁴	Identifying and designing potential areas to be protected within a region ¹⁰⁷	Identifying hotspots of species highly exposed ¹⁹	Assessing which of the populations of a species will experience the greatest changes in its distribution ¹⁰⁴	Predicting spatial overlap between the current and future range of a species ¹⁰⁸	Modelling possible future community assemblages ¹⁰⁹
Examples of objectives: mechanistic	Representing postglacial expansions from glacial refugia ¹¹⁰	Quantifying population reductions in recent times due to changes in sea ice extent ⁴¹	Predicting survival under future climate change ¹¹¹	Determining climatic factors that affect reproductive success of a reintroduced species ¹¹²	Exploring the range margin dynamics for species of conservation concern within a region ⁴⁰	Assessing species thermal tolerances across their range ¹¹³	Assessing the extinction risk of a population at the margins of a species' range ⁴⁰	Assessing the impacts of sea level rise on a coastal species ¹¹⁴	Modelling prey-predator dynamics under future climatic conditions ⁴⁵

	Understanding the effects of changes in CO ₂ concentration on plants ¹¹⁵	Determining population viability due to an increase in frequency of extreme climatic events during the last decades ⁴³	Assessing species' probability of extinction by 2100 ⁴¹	Predicting the probability of extinction of a keystone species within a site ⁴²	Exploring the extinction risk of a species in part of its range ³⁹	Predicting changes in fitness due to global warming globally ⁶⁸	Determining the extinction risk of a threatened subspecies ³⁴	Estimating species' abundance in the future under climate change ¹¹⁶	Predicting future expansions of invasive species ¹¹⁷
Examples of objectives: TVA	Identifying trends of past extinctions related to life history traits ¹¹⁸	Identifying taxonomic groups that currently retain high numbers of sensitive and unadaptable species ⁷⁸	Identifying sensitive species living in areas that are likely to become highly exposed in the future ¹¹⁹	Prioritizing conservation actions at the local scale ¹²⁰	Making an assessment of species vulnerability within a country ⁸⁰	Identifying species with the greatest relative vulnerability to climate change ⁷⁸	Identifying potential adaptive characteristics of an isolated subspecies ³⁵	Identifying the traits that make a species most vulnerable to climate change ¹²⁰	Identifying the most vulnerable species to climate change within a taxon ²⁰
	Predicting the response of species, that share life history traits with past extinct/impacted species, to future climatic changes ¹²¹	Identifying the characteristics of species that played the most important role in determining reductions/extinctions in recent years ¹⁴	Identifying unadaptable species with the largest predicted range shifts in the coming decades ⁸³	Understanding which component of vulnerability is prevalent for a species within a site ¹²²	Understanding how traits relate to changes in occurrence of species within a freshwater basin subject to droughts ¹¹	Identifying areas with the greatest number of vulnerable species at the global scale ¹⁴	Identifying potentially vulnerable subspecies/populations/varieties with relatively unknown distribution ³⁶	Assessing species' adaptive capacity/resilience ¹⁴	Selecting different adaptation strategies according to the relative vulnerability of different species ⁷⁸

758 *References from 101 to 122 are listed in the Supplementary material.

759

760 **Box 1 | Data availability**

761 Once clear objectives have been established, and the potential approaches identified, another
762 consideration for selecting the most appropriate method is to consider the types of data available.
763 The financial resources, time, expertise and input data required for each method are likely to mean
764 that just one or, at best, a few approaches are feasible. When fine scale data on species occurrence
765 are available (e.g. point localities), correlative and mechanistic niche models may be applied. To
766 build these types of models, adequate climate data covering different time periods are also needed.
767 For example, paleoclimatic reconstructions for Paleocene and Holocene, as well as current and
768 future projections, are already available under different resolutions and time intervals (e.g.^{123,124}).

769 Where relevant life-history data (e.g. data on species' biology, ecology, physiology,
770 demography) are available; (see ecology and trait databases for birds¹²⁵, mammals^{81,126} and
771 amphibians¹²⁷), trait-based or mechanistic approaches could facilitate, for example, the
772 identification of resilient and/or adaptable species, thus aiding in prioritization¹¹. Moreover, these
773 kinds of data are necessary to develop mechanistic niche models to refine species' distribution based
774 on the mechanisms that species themselves develop to cope with global warming¹³. Often this type
775 of empirical data will be lacking. Rather than abandon modelling and informing conservation
776 decisions in these cases, structured expert elicitation approaches offer an interim way of estimating
777 key species demographic and life-history parameters^{128,129}.

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