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Article:

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CLIMATE CHANGE VULNERABILITY ASSESSMENT OF SPECIES

Article Type: Overview

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ABSTRACT

Assessing species' vulnerability to climate change is a prerequisite for developing effective strategies to conserve them. The last three decades have seen exponential growth in the number of studies evaluating how, how much, why, when, and where species will be impacted by climate change. We provide an overview of the rapidly developing field of climate change vulnerability assessment (CCVA) and describe the key concepts, terms, important steps and considerations. We stress the importance of identifying the full range of pressures, impacts and their associated mechanisms that species face and using this as a basis for selecting the appropriate assessment approaches for quantifying vulnerability. We outline four CCVA assessment approaches, namely trait-based, correlative, mechanistic and combined approaches and discuss their use. Since any assessment can deliver unreliable or even misleading results when incorrect data and parameters are applied, we discuss finding, selecting, and applying input data and provide examples of open-access resources. Because rare, small-range, and declining-range species are often of particular concern and pose significant challenges for CCVA, we describe alternative ways to assess them. We also describe how CCVAs can be used to inform IUCN Red List assessments of extinction risk. Finally, we suggest future directions in this field and propose areas where research efforts may be particularly valuable.

30 **GRAPHICAL/VISUAL ABSTRACT**

STEPS FOR CARRYING OUT
CLIMATE CHANGE VULNERABILITY ASSESSMENT OF SPECIES

1. Define the **GOALS & OBJECTIVES** of your CCVA — Tbl 5, S1

2. Consider the climate change pressures and their mechanisms of impact to **IDENTIFY ALL LIKELY IMPACTS** on species — Pressures: Fig 3 / Mechanisms: Fig 5, Tbl2 / Impacts: Fig 4, Tbl 1

3. **QUANTIFY THESE IMPACTS**

Stage 1: Assess all likely mechanisms & impacts using **EXPERT KNOWLEDGE** and **TRAIT-BASED**[1] assessment
Result → Ranks or categories of species' vulnerability

Stage 2: Improve assessment of changing habitat suitability using **CORRELATIVE**[2] assessment (incl. combined correlative-trait[3])
Result → Potential distribution & population changes

Stage 3: Improve assessment of any mechanism and impact using **MECHANISTIC**[4] assessment (incl. mechanistic-correlative-trait combinations[3])
Result → Extinction probability, Potential distribution & population changes

Increasing resource requirements

Methods of application:
[1] Tbl S2
[2] Tbl S3
[3] Tbl S5
[4] Tbl S4

31
32 **Caption:**

33 Assessing species' vulnerability to climate change is becoming a prerequisite for
34 conservation planning, but approaches for doing so are varied. Navigate a sound path
35 through do's and don'ts, and explore resources and future perspectives in this exciting field.

2

36

INTRODUCTION

In 2016, the Bramble Cay Melomys (*Melomys rubicola*) became the first documented case of climate-induced extinction among contemporary mammals (Gynther *et al.*, 2016; IUCN, 2017). This Australian rodent, endemic to the small, low-elevation island of Bramble Cay, near Papua New Guinea, was periodically recorded from 1978 to late 2009 (Limpus *et al.*, 1983; Latch, 2008; Gynther *et al.*, 2016). Over the last decade, waves overtopping at least parts of the island due to rising sea levels, along with increasingly frequent and severe storm surges, led to dramatic habitat loss and possibly direct mortality of individual animals. Intensive searches in 2011 and 2014 failed to detect any remaining individuals (Gynther *et al.*, 2016). The species is not represented in *ex situ* collections and is therefore considered extinct.

The Bramble Cay Melomys joins a rapidly growing number of species for which the impacts of anthropogenic climate change have been documented. These species span: different biological kingdoms, including plants and animals; most latitudes, including polar, temperate, subtropical and tropical; many ecosystems, including those of the marine, freshwater and terrestrial realms; all the principal terrestrial biomes, from tundra to equatorial rainforest; and most habitat types, including coral reefs, forests, deserts, grasslands and wetlands (e.g. Gardner *et al.*, 2015; Hughes *et al.*, 2003; Pounds *et al.*, 2006; Chen *et al.*, 2009; Doney *et al.*, 2011; Whinam *et al.*, 2014; Mason *et al.*, 2015a; Ramula *et al.*, 2015; Scheffers *et al.*, 2016). Within species, impacts have been shown at levels from genes and individuals to populations, and changes in composition of communities and in inter-specific interactions are also prevalent (e.g. Gardner *et al.*, 2015; Chen *et al.*, 2011; Ramula *et al.*, 2015; Scheffers *et al.*, 2016). These impacts have occurred at global mean temperature increases of less than 1°C, yet without major reductions in emissions of carbon dioxide and other greenhouse gases, a rise of 2°C or more is increasingly probable. As a result, many more impacts including species declines and extinctions are likely, with the potential to undermine ecosystem health and function (Martin & Watson, 2016; Pecl *et al.*, 2017).

How can further climate change-driven extinctions and negative impacts be minimised? The emerging field of 'climate-smart' nature conservation aims to update conservation principles and practice to lessen climate change's impact on biodiversity (Stein *et al.*, 2014). Fundamental to choosing effective species' conservation strategies is the need to address the questions: 'What effects are climate changes already having?' and 'What is likely to happen in the future?'. In conservation terms, this requires robust assessments of species' vulnerability to climate change. Questions often asked in the context of climate change impacts on species include 'Which species?', 'How?', 'How much?', 'When?', 'Where?' and 'What remains unknown?' Performing a climate change vulnerability assessment (CCVA) underpins subsequent identification, prioritisation and implementation of adaptation management options (Glick *et al.*, 2011; Foden & Young, 2016) (Figure 1). Answering these questions is of critical importance if we are to identify modifications needed for current conservation strategies and interventions.

3

74   Over the past decade interest in assessing the climate change vulnerability of biodiversity has

75   increased explosively among managers, planners, policy makers, and researchers working at local,

76   regional and global scales. Nonetheless, predicting climate change impacts on biodiversity remains a

77   major challenge to science (Pereira *et al*., 2010; Pacifici *et al*., 2015), and studies comparing

78   assessments with observed changes have met with limited success (Wheatley *et al*., 2017). Further

79   research is required. This review responds to the proliferation of literature on individual species

80   assessments that predominate over assessments at other biological scales. Based on a collective

81   effort to develop practical, user-friendly guidance for CCVA of species (Foden & Young, 2016), we

82   share key concepts, and guide readers through commonly-used concepts and terms, steps for

83   carrying out assessments, and selecting methods, as well as approaches for communicating and

84   applying results. We outline resources available for users seeking more detailed or specific guidance.

85   Finally, we discuss use of the results in Red List assessments of extinction risk, as well as promising

86   new directions in this rapidly developing field. Since CCVA ultimately feeds into the wider context of

87   identifying leverage points for minimising negative impacts of the climate change crisis on

88   biodiversity (Figure 1), we consistently draw readers' attention back to this conservation context.

89   Vulnerability assessment is primarily about identifying potential problems that must be planned for

90   and addressed by appropriate environmental and conservation policies and actions.

91

92   *Figure 1: Steps for developing climate change adaptation strategies (Adapted from Glick et al. (2011))*

93

94

95   **THE EMERGENCE OF CLIMATE CHANGE VULNERABIILITY ASSESSMENT**

96   Although the influence of the atmospheric concentration of carbon dioxide on global climate had

97   been identified already in the late 19th century (Arrhenius, 1896), it was only during the late 1970s

98   that concern about human impacts upon the climate system really began to grow. This concern grew

99   rapidly such that by the mid-1980s there was a steady flow of scientific publications, including such

4

100   landmarks as the SCOPE 29 volume (Bolin *et al.*, 1986) that addressed the potential impacts upon

101   ecosystems both of projected climate changes and of the direct effects of increasing carbon dioxide

102   concentration. In 1987 the International Council of Scientific Unions established the International

103   Geosphere–Biosphere Programme that stimulated international research organised around six core

104   projects, including 'Global Change and Terrestrial Ecosystems', and that led to numerous influential

105   publications (e.g. Walker & Steffen, 1996). The rapid growth in international concern also led to the

106   establishment in 1988 of the Intergovernmental Panel on Climate Change (IPCC) that produced its

107   first report in 1990 in which it discussed, albeit briefly, the potential impacts upon biodiversity and

108   identified the potentially most vulnerable ecosystems (Street *et al.*, 1990). The implications for

109   conventional approaches to biodiversity conservation began to be discussed around the same time

110   (e.g. Hunter, Jacobson, & Webb, 1988; Huntley & Webb III, 1988) and the lessons that could be

111   learned from studies of Quaternary palaeoecology also began to be discussed (e.g. Huntley & Webb

112   III, 1988; Huntley, 1990, 1991). Subsequently the volume edited by Peters & Lovejoy (1992)

113   represented a key milestone on the road towards formalised assessments of species' vulnerabilities

114   to climate changes.

115

116   Climate change vulnerability assessment as a field emerged in the 1990s, drawing on several

117   disparate disciplinary traditions, including natural hazard and disaster planning, climate change

118   effects research, and endangered species conservation. The concepts behind vulnerability were

119   originally and most fully developed in relation to risks from natural hazards to people and

120   communities. Indeed, the field of climate adaptation has been heavily influenced by the work of

121   such natural hazards researchers as Gilbert F. White and colleagues, who emphasized the

122   importance of social and technological 'adjustments' to these hazards (Burton *et al.*, 1993). Building

123   on such disaster-related usage, early applications of vulnerability assessment in a climate change

124   context primarily focused on susceptibility of people, infrastructure and economies to harm (Dow,

125   1992; IPCC, 1996). Adger (2006) offered perhaps the most influential distillation of climate change

126   vulnerability in a socioecological context, noting that 'the key parameters of vulnerability are the

127   stress to which a system is exposed, its sensitivity, and its adaptive capacity.'

128

129   Biogeographers, ecologists and conservation biologists began to explore the potential impacts of

130   climate change on species and ecosystems during the early and mid-1990s (e.g. Lindenmayer *et al.*,

131   1991; Huntley *et al.*, 1995; Sykes & Prentice, 1995; Sykes *et al.*, 1996). Around the same time

132   observed effects of climate change on species' distributions began to be documented (e.g. Grabherr

133   *et al.*, 1994; Parmesan, 1996; Parmesan *et al.*, 1999) and the interacting effects upon species of

134   climate change and habitat availability were discussed (e.g. Hill *et al.*, 1999). By the early 2000s, a

135   range of effects of climate change on species was being widely documented (e.g. Hughes, 2000;

136   Parmesan & Yohe, 2003), leading to more explicit interest in determining 'which species, habitats

137   and regions are most at risk from climate change' (Pearson & Dawson, 2003), and the realisation

138   that substantial numbers of species could be at risk of extinction (Thomas *et al.*, 2004). This in turn

139   led to the application and modification of existing vulnerability frameworks (e.g. Schroter *et al.*,

140   2005; Adger, 2006) for assessing natural systems, including plant and animal species (Williams *et al.*,

141   2008; Pacifici *et al.*, 2018). Such applications were also informed by the rich tradition of assessing

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142 species' extinction risk (e.g. the IUCN Red List (Mace & Lande, 1991)) and efforts to integrate
143 knowledge about interacting threats to species persistence.

144

145 **Vulnerability**
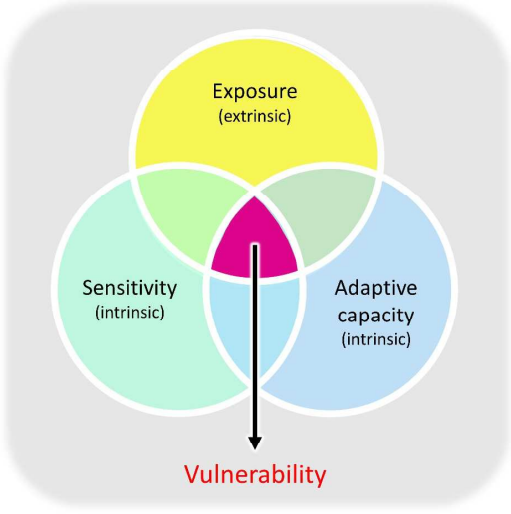
146 In the field of conservation biology, vulnerability is generally viewed as 'the degree to which a
147 system is susceptible to, and unable to cope with, the adverse effects of climate change' (IPCC,
148 2007). As such, 'it is a function of the character, magnitude and rate of climate change to which the
149 system is exposed, its sensitivity and its adaptive capacity' (IPCC, 2007). Although an alternative
150 definition was presented in the IPCC Fifth Assessment Report (IPCC, 2014), this has not been widely
151 adopted within the conservation community; accordingly, here we use the former definition but
152 discuss in Box 1 the differences with the more recent definition.

153

154

Box 1. Vulnerability: Old vs. New Definitions

We note a shift in definitions between the IPCC's Fourth and Fifth Assessment Reports. In the former, the overall measure of concern (vulnerability), is defined as a function of intrinsic properties, namely sensitivity and adaptive capacity, and the magnitude and rate of climate change to which the system is exposed. In the latter, 'risk' is considered the overall measure of concern, with its contributing factors being intrinsic properties of vulnerability and exposure, and the extrinsic forcing agent defined as 'hazard'. The IPCC Fourth Assessment (2007) definition was widely adopted by the conservation community, with little attention paid to the revised Fifth Assessment (2014) definition in the conservation literature. We therefore use the Fourth Assessment definition in this review.

IPCC Fourth Assessment terms (2007)	IPCC Fifth Assessment terms (2014)

Figure 2a. According to the IPCC Fourth Assessment (2007) and common usage in the field of CCVA of species, vulnerability to climate change results from the interaction of exposure and sensitivity with adaptive capacity (adapted from IPCC, 2007).

Figure 2b. According to the IPCC Fifth Assessment (2014), risk of climate-related impacts results from the interaction of climate-related hazards with the vulnerability and exposure of human and natural systems (adapted from IPCC (2014)).

Overarching measures of concern	
Vulnerability. The extent to which biodiversity is susceptible to or unable to cope with the adverse effects of climate change. It is a function of the character, magnitude and rate of climate change to which the system is **exposed**, its **sensitivity** and its **adaptive capacity** (IPCC, 2007) *(Differs from IPCC, 2014a).*	**Risk.** The probability of harmful consequences resulting from climate change. Risk results from the interaction of **vulnerability, exposure,** and **hazard**. Risk is often represented as *probability* of occurrence of hazardous events or trends multiplied by the *impacts* if these events or trends occur (IPCC, 2014) *(not defined in 2007)* **Impact.** The effects, consequences or outcomes of climate change on natural and human systems. It is a function of the interactions between climate changes or **hazardous** climate events occurring within a specific time period and the **vulnerability** of an **exposed** society or system (IPCC, 2014) *(Differs from IPCC, 2007)*
Intrinsic Contributing Factors	
Sensitivity. Sensitivity is the degree to which a system is affected, either adversely or beneficially, by *climate variability* or change (IPCC, 2007, 2014) **Adaptive Capacity.** The potential, capability, or ability of a species, ecosystem or human system to adjust to	**Vulnerability.** 'The propensity or predisposition to be adversely affected. In this usage, vulnerability encompasses a variety of concepts, particularly **sensitivity** to harm and **lack of capacity to cope and adapt.'** (IPCC, 2014) *(Differs from IPCC, 2007).*

7

climate change, to moderate potential damage, to take advantage of opportunities, or to respond to the consequences (IPCC, 2007, 2014)	Exposure. The *presence* of people, livelihoods, species or ecosystems, environmental functions, services, and resources, infrastructure, or economic, social, or cultural assets in places and settings that could be adversely affected (IPCC, 2014) *(Not defined in IPCC, 2007)*
External Contributing Factors	
Exposure. Exposure describes the nature, magnitude and rate of climatic and associated environmental changes experienced by a species (Dawson *et al.*, 2011; Foden *et al.*, 2013; Stein *et al.*, 2014) *(Not defined in IPCC, 2007)*	Hazard. The potential occurrence of a natural or human-induced physical event or trend or physical impact that may cause loss of life, injury, or other health impacts, as well as damage and loss to property, infrastructure, livelihoods, service provision, ecosystems, and environmental resources. In [the IPCC Fifth Assessment] report, the term *hazard* usually refers to climate-related physical events or trends or their physical impacts (IPCC 2014)) *(Not defined in IPCC, 2007).*

155

156   **Exposure**

157   Exposure refers to the nature, magnitude, and rate of extrinsic climatic and associated
158   environmental changes experienced by a species (Dawson *et al.*, 2011; Foden *et al.*, 2013; Stein *et*
159   *al.*, 2014). Describing and quantifying exposure to climate change requires understanding its
160   components and unpacking an often-conflicting 'entanglement' of terminology and concepts
161   (Oesterwind *et al.*, 2016). While some studies describe climate change as a driver (e.g. Millenium
162   Ecosystem Assessment, 2005), others have defined it as a pressure (Omann *et al.*, 2009) or a threat
163   (e.g. Salafsky *et al.*, 2007). Given the conservation context in which CCVA of species is conducted, we
164   recommend an approach consistent with the Driver-Pressure-State-Impact-Response (DPSIR)
165   framework (European Environment Agency, 1995; Holten-Andersen *et al.*, 1995) that is widely
166   applied in conservation and other disciplines for structuring and communicating policy-relevant
167   research (Kristensen, 2004; Svarstad *et al.*, 2008).

168

169   *Drivers* are the highest order phenomena governing change; they typically encompass societal
170   demands or needs (e.g. economic, social, and political) and natural factors that are independent of
171   anthropogenic causes (e.g. earthquakes, tectonic drift) (Maxim *et al.*, 2009; Oesterwind *et al.*, 2016).
172   A key characteristic of drivers is that they are beyond direct control or management (Oesterwind *et*
173   *al.*, 2016). In the context of climate change and biodiversity, drivers are the factors leading to
174   greenhouse gas emissions, including society's needs for energy, transport and food, as well as
175   contributing natural factors such as volcanic eruptions.
176
177   Climate change drivers result in *pressures* which may cause state changes or impacts on human and
178   natural systems. In the context of climate change and species, we propose a pressure classification

8

179 that includes three broad categories (Figure 3). *Abiotic pressures* include: climate changes driven by
180 changes in atmospheric concentrations of greenhouse gases (e.g. increased temperatures, altered
181 drought frequency); resulting effects on the physical environment (e.g. sea level rise, melting ice,
182 increased severity of storm surges); and, direct effects of the changes in greenhouse gas
183 concentrations (e.g. ocean acidification as a result of the increased atmospheric concentration of
184 carbon dioxide). *Biotic pressures* result from changes in ecological processes (Ockendon *et al.*, 2014)
185 and include those mediated through changes in habitat availability or community composition (e.g.
186 increased competition from alien species), as well as direct effects of the changes in greenhouse gas
187 concentrations (e.g. differential effects of elevated carbon dioxide levels on productivity of plants
188 using alternative photosynthetic pathways). Finally, various societal actions resulting from climate
189 change, including both from climate change mitigation (e.g. expansion of biofuel production,
190 renewable energy technologies) and adaptation (e.g. changing land use, construction of dams and
191 sea walls, water abstraction) may exert *human response pressures* on species that, although poorly
192 recognised in vulnerability assessments, potentially have large impacts upon biodiversity (Turner *et*
193 *al.*, 2010; Watson & Segan, 2013; Maxwell *et al.*, 2015). This category also includes climate change
194 driven exacerbation of historical human pressures such as harvesting and persecution. We note that
195 pressures and drivers may be variously interpreted in ecological contexts, and that several authors
196 have classified pressures as 'direct' (i.e. abiotic) and 'indirect' (i.e. biotic, and in some cases including
197 human-mediated responses)(e.g. Chapman *et al.*, 2014; Ockendon *et al.*, 2014; Segan *et al.*, 2015).
198 However, strong interactions and feedbacks between almost all contributing pressures (Figure 3)
199 suggest that it is more realistic to consider biological responses as emerging from a complex network
200 of interacting physical, biological and human processes.
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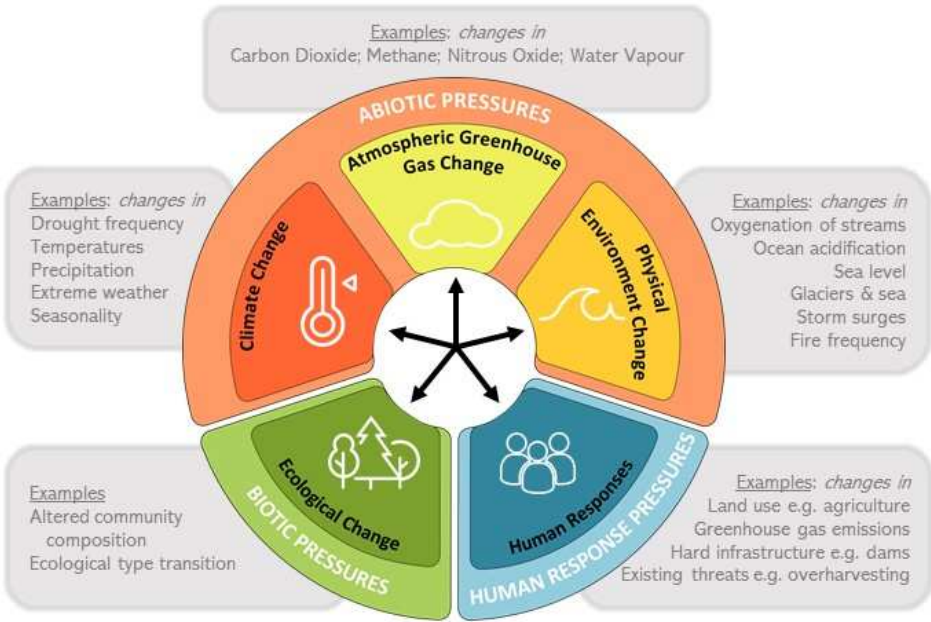
203 *Figure 3. Climate change related pressures on species, showing those originating from abiotic, biotic*
204 *and human response causes.*

205

206 **Potential impacts and their mechanisms**

207 Pressures exert influence on the *state* of systems (Oesterwind *et al*., 2016) and may thereby lead to
208 *impacts* on them (Svarstad *et al*., 2008). The extent of impacts on species resulting from climate
209 change associated pressures depends upon the intrinsic and external factors contributing to the
210 species' vulnerability and may be positive, negative or a combination of both. In the context of CCVA
211 of species, the focus is species' vulnerability to climate change-driven extinction, and the impacts are
212 factors that influence this. Key parameters used by the IUCN Red List (IUCN, 2017) to assess a
213 species' extinction risk are characteristics of, and changes in, its population size and distribution
214 extent. While these parameters are appropriate at the species level, we note that they result from
215 impacts on individuals that differ from one another both genetically and phenotypically with respect
216 to their morphological, physiological, behavioural and life-history attributes (Figure 4 and Table 1).
217 Individual-level impacts influence subpopulation characteristics, including local abundance and
218 metapopulation dynamics, that in turn determine species-level parameters, including extinction risk
219 (Griffiths *et al*., 2010). It is important to realise that climate change will often have contrasting
220 impacts on different organisms and local- or subpopulations of a species in different parts of their
221 overall distribution. Thus, impacts are likely to be positive towards the 'leading edge' of a species'
222 distribution, but negative towards the 'trailing edge', where leading and trailing edge are defined by
223 the geographical gradient and direction of change of a climatic variable. The net results of these
224 individual subpopulation-level impacts are changes in the species' overall population and
225 distribution.
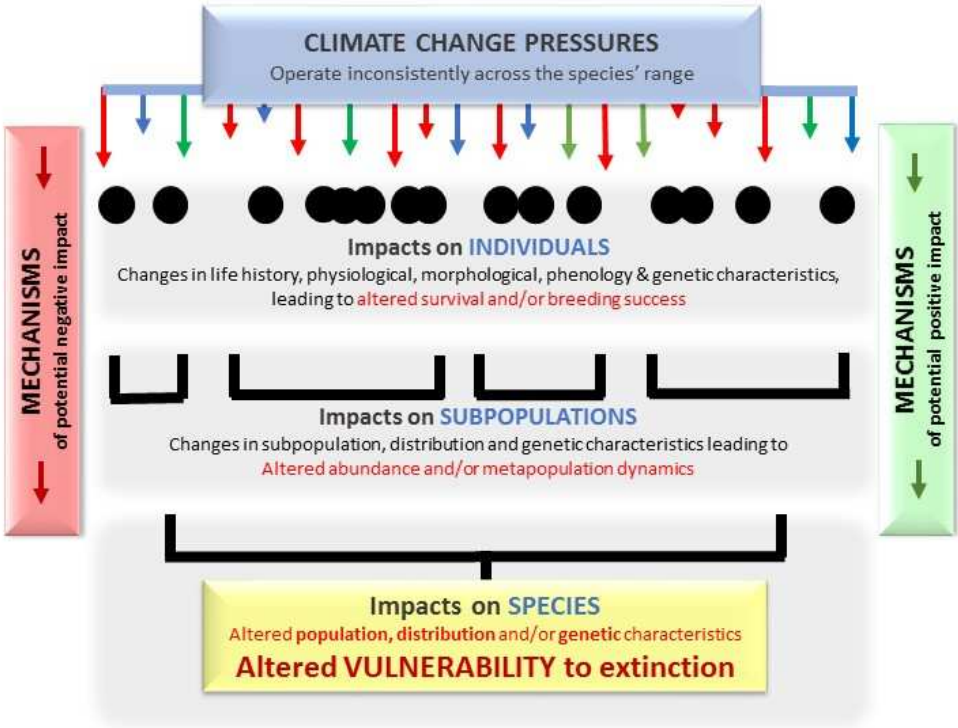
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Figure 4. Potential climate change impacts on species include the species-level population and range changes that underpin extinction risk. These changes are driven by changes at individual and subpopulation levels.

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*Table 1. Summary of types of climate change **impacts** on species, including those that are both positive and negative, with examples of where they have been documented. Further examples are documented in Bellard et al. (2012) and Scheffers et al. (2016). Here we define populations as the total number of individuals of the species and subpopulations as geographically or otherwise distinct groups within the population (IUCN SSC Standards and Petitions Subcommittee, 2017).*

Impacts	Illustrative examples
SPECIES LEVEL	

1. **Population characteristics**
  1.1. Changes in population size
  1.2. Changes in proportion of mature individuals
  1.3. Changes in sex ratio
  1.4. Changes in magnitude and/or frequency of population fluctuations
  1.5. Number of subpopulations
	Gynther *et al.*, 2016

2. **Range characteristics** 2.1. Changes in range size	Hickling *et al.*, 2006; Tingley *et al.*, 2009; Chen *et al.*, 2011;

2.2. Changes in range location 2.3. Level of fragmentation	Poloczanska *et al.*, 2013; Mason *et al.*, 2015
3. Genetic characteristics 3.1. Changes in genetic diversity (e.g. due to stochastic effects of changes in population size; inter-breeding with newly encountered species, especially congeners; loss of subpopulations; and restrictions on gene flow) 3.2. Changes in allele frequencies (e.g. due to adaptive selection and stochastic effects of changes in population size)	Bradshaw & Holzapfel, 2006; Forcada & Hoffman, 2014; Potts *et al.*, 2014
SUBPOPULATION LEVEL	
4. Subpopulation characteristics 4.1. Changes in sizes of subpopulations 4.2. Changes in the probability of local extinction and/or colonisation 4.3. Changes in subpopulation sex ratio 4.4. Changes in subpopulation age structure 4.5. Changes in magnitude and/or frequency of subpopulation fluctuations	Franco *et al.*, 2006; Martay *et al.*, 2017
5. Range characteristics 5.1. Changes in range sizes of subpopulations 5.2. Changes in range locations of subpopulations	Bennie *et al.*, 2013
6. Genetic characteristics 6.1. Changes in genetic diversity 6.2. Changes in allele frequencies 6.3. Changes in rates of gene flow between subpopulations	Kutschera *et al.*, 2016; Vincenzi *et al.*, 2017
INDIVIDUAL LEVEL	
7. Life-history characteristics 7.1. Changes in growth rates 7.2. Changes in duration of developmental stages 7.3. Changes in reproductive output and success 7.4. Changes in survival rates, and hence in longevity	Forchhammer *et al.*, 1998; Barbraud & Weimerskirch, 2001; Aars & Ims, 2002; Ludwig *et al.*, 2006; Foley *et al.*, 2008; Robinson *et al.*, 2009; Martin & Maron, 2012
8. Morphological characteristics 8.1. Changes in body size 8.2. Changes in body shape	Rode *et al.*, 2010; Cheung *et al.*, 2012; Baudron *et al.*, 2014; Caruso *et al.*, 2014
9. Physiological characteristics 9.1. Changes in phenotypic plasticity 9.2. Changes in metabolic rate 9.3. Changes in stress tolerance 9.4. Changes in disease susceptibility	Garamszegi, 2011; Crozier & Hutchings, 2014; Rangan *et al.*, 2015
10. Phenological characteristics 10.1. Changes in phenology (i.e. in seasonal timing of events, including migration, hibernation, flowering, bud burst, spawning, etc.) 10.2. Changes in direction and/or distance of seasonal migration 10.3. Changes in circadian (i.e. daily) pattern of activity	Both *et al.*, 2010; Thackeray *et al.*, 2010; Todd *et al.*, 2010; Møller *et al.*, 2011; Lane *et al.*, 2012; R. Kearney, 2013

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(e.g. a shift from diurnal to crepuscular or nocturnal activity)	

11. Genetic characteristics
    11.1.   Changes in gene expression (e.g. due to epigenetic processes)
    11.2.   Heterozygosity
	Bradshaw & Holzapfel, 2001; Hill & Henry, 2011; Geerts *et al.*, 2015; Pacifici *et al.*, 2015; de Pous *et al.*, 2016

236

237 Understanding the *mechanisms* of potential climate change impacts on species, that is, the chain of
238 events between the exertion of the pressure and the potential impacts at species level, is
239 particularly valuable. Firstly, the degree of confidence associated with a projected climate change
240 impact is increased if there is evidence that the impact is underpinned by a known mechanism that
241 also has been shown to be operating. Secondly, it can help identify appropriate targets for
242 conservation interventions, thus allowing development of strategies to disrupt mechanisms
243 underpinning negative impacts. Individual mechanisms may act alone, or in combinations that may
244 be synergistic, antagonistic or neutral; mechanisms may also operate in different ways and to
245 different extents at different times and/or locations. We propose here five general types of climate
246 change impact mechanisms (Table 2). The relationship between impacts and the mechanisms driving
247 climate change vulnerability of species, as shown in Figure 5, are mediated by species' unique
248 sensitivities and adaptive capacities.

249

250 *Table 2. Five potential mechanisms of climate change impacts that may operate on organisms,*
251 *subpopulations and thereby species. These may have positive and/or negative impacts on species'*
252 *vulnerability to climate change.*

POTENTIAL MECHANISMS OF IMPACTS ON SPECIES	**Documented examples** (+ve) or (-ve)
1. Organisms' **physiological preferences** or limits become decreasingly or increasingly aligned with changing **environmental conditions.**	Kullman, 2007; Oswald *et al.*, 2008; Pérez-Ramos *et al.*, 2010; Sinervo *et al.*, 2010; Beever *et al.*, 2011; Cahill *et al.*, 2013
2. Organisms' **habitat and microhabitats** change in quality or availability leading to changes in the availability and quality of key resources. Examples of microhabitats include caves for roosting bats and boulders for desert reptiles.	Munday, 2004; Trape, 2009; Regehr *et al.*, 2010; Rode *et al.*, 2010; Bond & Midgley, 2012; Martin & Maron, 2012
3. Organisms experience changes in **interspecific interactions**. This includes with **beneficial species** (e.g. prey, mutualists, hosts, pollinators, dispersers), **detrimental species** (e.g. competitors, predators, parasites, pathogens) and those that are currently **neutral** but may become beneficial or	Biesmeijer *et al.*, 2006; Schweiger *et al.*, 2008; Durance & Ormerod, 2010; Pearce-Higgins *et al.*, 2010

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detrimental in the future.	
4. Organisms experience change in **phenology** such that the timing of beneficial events or interactions are disrupted or enhanced.	Visser *et al.*, 2006; Fryxell & Sinclair, 1988; Ludwig *et al.*, 2006; Altwegg *et al.*, 2012
5. Organisms experience changes in interactions with **non-climate change-driven threats** such that they are exacerbated (e.g. overharvesting, invasive species, land use changes)	Frederiksen *et al.*, 2004; Walther *et al.*, 2009; Schweiger *et al.*, 2010; Van Zuiden & Sharma, 2016; Kovach *et al.*, 2017
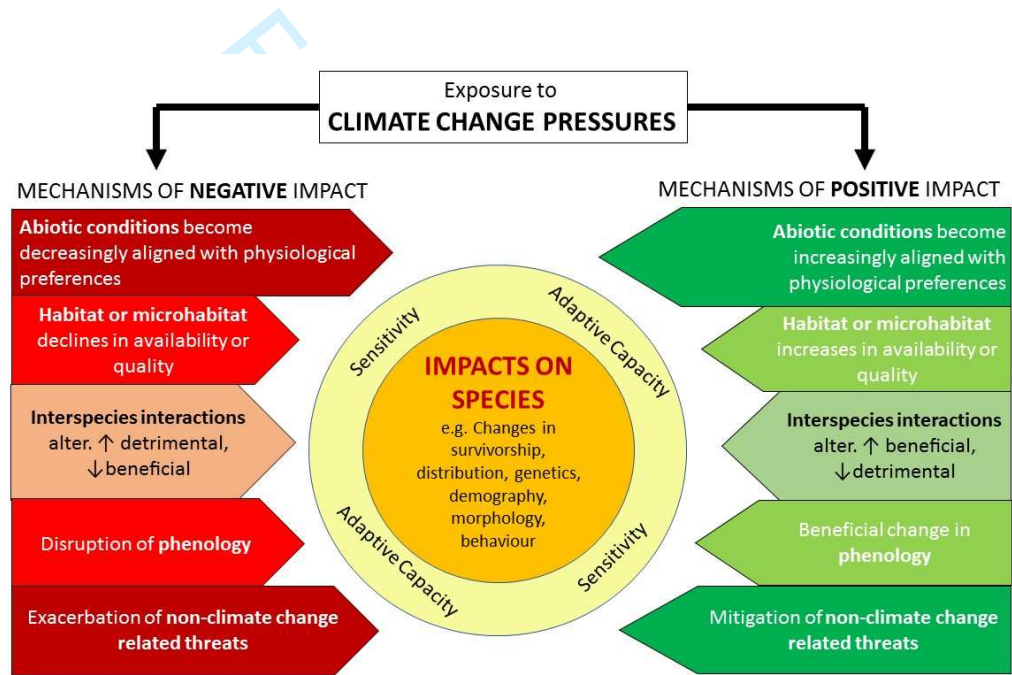
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Figure 5. Mechanisms describe the pathways through which climate change pressures may exert impacts on species. These impacts may have positive and/or negative impacts on the species and are mitigated or exacerbated by species' individual sensitivities and adaptive capacities.

Sensitivity

Ssensitivity refers to the degree to which a system [or species] is affected, either adversely or beneficially, by climate change (IPCC, 2007, 2014). While exposure, drivers, and pressures describe factors that are external to the species, sensitivity describes *intrinsic* attributes that are recognised to moderate and/or exacerbate the impact of those pressures on a species response (Jiguet *et al.*,

14

268 2007; Dawson *et al.*, 2011; Nicotra *et al.*, 2015). The types of attributes that affect species' sensitivity
269 to climate change have been categorised in various ways (e.g. Keith *et al.*, 2008; Visser, 2008;
270 Williams *et al.*, 2008), but typically include: A) specialized habitat and/or microhabitat; B)
271 environmental tolerances or thresholds that are likely to be exceeded due to climate change; C)
272 dependence on environmental triggers that are likely to be disrupted by climate change; D)
273 dependence on interspecific interactions that are likely to be disrupted by climate change; E) rarity;
274 F) sensitive life history; and F) high exposure to other pressures (Table 3). These categories of
275 species attributes are not exhaustive nor mutually exclusive and are proposed simply to aide
276 understanding and assessment of how species are sensitive to climate change. Evaluating sensitivity
277 attributes requires detailed knowledge of focal species and the systems where they function. Where
278 such knowledge is lacking, or the evidence linking an attribute to climate change sensitivity is weak,
279 sensitivity assessments may have a high degree of uncertainty.
280

281 *Table 3. Attributes associated with species' sensitivity to climate change (adapted from Foden et al.,*
282 *(2013)).*

Sensitivity Attributes
A. **Specialised habitat and/or microhabitat requirements.** As climate change-driven environmental changes unfold, species that are less tightly coupled to specific conditions and requirements are likely to be more resilient because they will have a wider range of habitat and microhabitat options available to them. Sensitivity is further increased for species with several life stages, each requiring different habitats or microhabitats (e.g. water-dependent larval amphibians), and in seasonally migratory species that use different habitats or microhabitats during different parts of their annual cycle of migration. We note, however, that this does not hold in all cases, and extreme specialization may allow some species to escape the full impacts of climate change exposure (e.g. deep sea fishes).
B. **Environmental tolerances or thresholds (at any life stage) that are likely to be exceeded due to climate change.** Species where the majority of populations already occur in conditions that are close to their physiological thresholds (e.g. for temperature or precipitation regimes, water pH or oxygen levels) are likely to be at higher risk from climate change (e.g. mid-latitude ectotherms)(Hoffmann *et al.*, 2013). However, even species with broad environmental tolerances may already be close to thresholds beyond which physiological function quickly breaks down (e.g. drought-tolerant desert plants (Foden *et al.*, 2007), high temperature-tolerant birds (Cunningham *et al.*, 2013)).
C. **Dependence on environmental triggers that are likely to be disrupted by climate change.** Many species rely on environmental triggers or cues to initiate life stages (e.g. migration, breeding, egg laying, seed germination, hibernation and spring emergence). While cues such as day length and lunar cycles will be unaffected by climate change, those driven by climate and season may alter in both their timing and magnitude, leading to asynchrony and uncoupling with environmental factors (Thackeray *et al.*, 2016) (e.g. mismatches between advancing spring food availability peaks and hatching dates (Both *et al.*, 2006)). Climate change sensitivity is likely to be compounded when different sexes or life stages rely on different cues, as well as by local adaptation of species to gradients in environmental triggers (e.g. Bennie *et al.*, 2010).

15

<table>
<tr><td>D.</td><td>Dependence on interspecific interactions that are likely to be disrupted by climate change. Climate change-driven alterations in species' ranges, phenologies and relative abundances may affect their beneficial inter-specific interactions (e.g. with prey, pollinators, hosts or symbionts) and/or those that have negative effects (e.g. with predators, competitors, pathogens or parasites). Species are likely to be particularly sensitive to climate change if, for example, they are highly dependent on beneficial interaction(s) with one or few particular species (e.g. Hutchings et al., 2018) and are unlikely to be able to substitute alternatives for these species (Møller et al., 2011).</td></tr>
<tr><td>E.</td><td>Rarity. The inherent vulnerability of small populations to Allee effects and catastrophic events, as well as their generally reduced capacity to recover quickly following local extinction events, suggest that many rare species will be more sensitive to climate change than common species. Rare species include those with very small population sizes, as well as those that may be locally abundant but are geographically highly restricted. Such small population size and/or restricted distribution may be intrinsic or the result of past and/or ongoing pressures that exert negative effects upon the species.</td></tr>
<tr><td>F.</td><td>Sensitive life history. Life history traits such as long generation length and slow growth rate have also been shown to be associated with heightened extinction risk under climate change (Pearson et al., 2014). Species that experience marked population fluctuations, particularly those where populations periodically 'crash' or pass through 'bottlenecks' , are particularly vulnerable to exacerbation of extreme events and/or climate variability at such times; on the other hand, species occurring in climates that have historically high vulnerability may possess life history characteristics that reduce vulnerability to further increases.. Species that become spatially concentrated at any stage of their life history (e.g. congregatory species, lekking species,) have low levels of adaptive variation and those that have temperature-dependent sex determination are also likely to be more sensitive.</td></tr>
<tr><td>G.</td><td>High exposure to other pressures. Climate change is likely to interact with a range of existing pressures, exacerbating their effects (e.g. increasing susceptibility to disease (Munson et al., 2008; Randall & van Woesik, 2015), increasing pressures from invasive species (Walther et al., 2009; Elmhagen et al., 2015), expansion of agriculture into some areas and abandonment in others (Hannah et al., 2013)). Species that are already declining due to non-climate change related pressures are therefore likely to be more sensitive to climate change. They may also be restricted to climate change-vulnerable parts of their former distributions (e.g. all higher latitude populations have gone extinct for non-climatic reasons). Pearson et al. (2014) found that decreasing population size and/or occupied area, as well as increasing range fragmentation, were associated with higher extinction risk under climate change.</td></tr>
</table>

283

Adaptive Capacity

285 Adaptive capacity has been defined as 'the potential, capability, or ability of a species, ecosystem or
286 human system to adjust to climate change, including changes in climate variability and extremes, so
287 as to moderate potential negative outcomes, to take advantage of opportunities, or to respond to
288 the consequences' (based upon IPCC WGII definitions, IPCC, 2007, 2014). The concept of adaptive
289 capacity was developed with respect to human systems, and with its origins in organizational theory
290 and sociology, emphasized system attributes such as governance, economic resources, technology,
291 and levels of education (Engle, 2011). The concept has been applied in an ecological context to
292 reflect those capacities of a system (whether a species or ecosystem) that enable it to adjust to or
293 cope with changing conditions. In practice, the application of adaptive capacity to species and other
294 natural resources has been challenging. In particular, many of the attributes that confer such
295 adaptability overlap with features also associated with 'sensitivity' (e.g. habitat specialization,
296 physiological tolerances, interspecific dependencies). At its root, the term 'adaptive' suggests
297 modification or adjustment, and thus the concept of adaptive capacity can perhaps best be thought

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298   of as the ability of a species to accommodate a given stressor or change through some form of
299   adjustment. The ability to adjust to changes is facilitated by high levels of phenotypic plasticity
300   dispersal ability, or 'evolvability' (associated with its genetic diversity). These in turn can enable a
301   species to adjust to new conditions by shifting locations, by modifying behaviours, physiology or life
302   history factors, or by evolving new and more 'adaptive' traits (Table 4).
303
304   Adaptive capacity includes both intrinsic and extrinsic elements, and in that sense is context specific.
305   Intrinsic factors include the dispersal, phenotypic and genetic attributes noted above. Extrinsic
306   factors, however, may constrain or promote the expression of those adaptive capabilities. For
307   example, even if a species has high dispersal capacity, if surrounding landscape conditions are
308   inhospitable to the species or its propagules, there will be limited opportunities for dispersal-based
309   coping. Indeed, the interplay between such intrinsic and extrinsic factors led Beever *et al*. (2016) to
310   suggest an analogy for adaptive capacity based on classic ecological niche theory, as first proposed
311   by Hutchinson (1957). In this conception, the *fundamental adaptive capacity* reflects a species'
312   intrinsic ability to accommodate climate change without significant genetic losses, large range
313   contractions or extinction, or intensive management intervention. The *realized adaptive capacity*, in
314   contrast, reflects how extrinsic factors constrain or limit expression of those intrinsic adaptive
315   capacity factors. Under this framework, adaptation can be viewed as those actions or efforts capable
316   of relaxing extrinsic constraints (particularly anthropocentric stressors) and shifting the realized
317   adaptive capacity further towards the fundamental condition.
318

319   *Table 4. Attributes associated with species' ability to adapt to climate change (adapted from Foden*
320   *et al. (2013) and Estrada et al. (2016)).*

ADAPTIVE CAPACITY ATTRIBUTES
A. Phenotypic plasticity. Changes in the phenotype expressed by an individual with a given genotype, perhaps as a result of epigenetic processes that alter gene expression, can enable adaptation to altered climate conditions. Such changes have been shown to play a key role in advances in the timing of avian breeding (Charmantier *et al*., 2008) and are likely to remain important in the future for some common insectivorous passerines (Phillimore *et al*., 2016), inferring high adaptive capacity for those species. Limited plasticity would require adaptive capacity to occur as a result of dispersal or evolution (below).
B. Dispersal ability. Estrada *et al*. (2016) outline a framework highlighting four key factors that influence species' range-shifts, namely: (i) **Emigration**. Many mobile species (e.g. many seasonally migrant birds) exhibit strong site fidelity or natal philopatry, most individuals returning to breed at or close to their natal site. Other species may show negative density-dependence of dispersal, with a greater proportion of individuals dispersing when population densities are lower, leading to more rapid colonisation of new areas (Altwegg *et al*., 2013).   (ii) **Dispersal** (movement ability):   Intrinsic dispersal ability: Species with low dispersal rates or low potential for long distance dispersal (e.g. land snails, ant and raindrop splash-dispersed plants) have low adaptive capacity since they are unlikely to be able to keep up with a shifting climate envelope. However, evidence of the rate and magnitude of past range shifts (e.g. Preece, 1997) showed that

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accidental dispersal by mechanisms to which the species shows no particular adaptations were more important than dispersal adaptations and typical dispersal distances in achieving rapid and large range shifts (e.g. Wilkinson, 1997; Wilkinson *et al.*, 2017).

Extrinsic limitations: Even where species are intrinsically capable of long distance or rapid dispersal, movement and/or successful colonisation may be reduced by low permeability or physical barriers along dispersal routes. Barriers to dispersal may be natural or anthropogenic and take various forms: oceans, large rivers or major highways can be barriers for terrestrial species; large waterfalls, dams or concentrations of pollutants can be barriers for freshwater species; tracts of unsuitable habitats or conditions can act as barriers for any species, for example, mountain ranges for lowland terrestrial species, arid areas for lacustrine and riverine freshwater species, cold ocean currents for marine species of warmer waters. Species for which little or no suitable habitat or 'climate space' is likely to remain (e.g. Arctic ice-dependent species) may also be considered to suffer from extrinsic dispersal limitations. Limited access to, or absence of, a key dispersal agent (e.g. by bird-dispersed plants) generally arises in relation to zoochory and results from the reduced range or population, or even the extinction, of key dispersal agents.

(iii) **Establishment.** A species' ability to establish at a new site depends on whether required resources available, making establishment by generalists more likely than by species with particular requirements for e.g. micro-habitats, food resources or mutualists. Some species exhibit allee effects, individual fitness being lower in small populations and hence limiting the species' ability to establish in new areas.

(iv) **Proliferation.** Species that are slow to reach reproductive maturity and/or that produce relatively small numbers of progeny/propagules have reduced dispersal ability simply because they produce fewer potentially dispersing entities. Sexually reproducing species that require a minimum of two individuals, one of each sex, to disperse to a given locality if a new population is to be established there have a lower dispersal ability than hermaphrodite species and/or species that reproduce asexually. Reproductive strategy, ecological generalisation and competitive ability play important roles in both successful establishment and proliferation.

C. Evolvability. Species' potential for rapid genetic change will determine whether evolutionary adaptation can result at a rate sufficient to keep up with climate change-driven changes to their environments. Species with low genetic diversity, often indicated by recent bottlenecks in population numbers, generally exhibit lower ranges of both phenotypic and genotypic variation. As a result, such species tend to have fewer novel characteristics that could facilitate adaptation to the new climate conditions.

Estimates of genetic diversity are becoming common and can now be readily obtained across the entire genome using SNP (single nucleotide polymorphism) markers which provide a picture not just of genetic diversity but also of historical processes acting on species and the likelihood of adaptive capacity across geographical gradients (Rellstab *et al.*, 2016). Evidence suggests that evolutionary adaptation is likely to be common across a few years in species with annual or shorter generation times (e.g. Lustenhouwer *et al.*, 2018). In animals and plants with longer generation times evolutionary adaptation may not keep up with climate change and populations may decline (Bay *et al.*, 2018) although where gene flow occurs across populations located along environmental gradients evolutionary adaptation may still occur.

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324   **CARRYING OUT CCVA OF SPECIES**

325   CCVAs typically follow a series of steps, which we illustrate in Figure 6 and outline below.

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328

329   *Figure 6. The approaches used to carry out each of the three assessment types and the metrics or*

330   *types of information of climate change vulnerability that they may produce.*

331

332
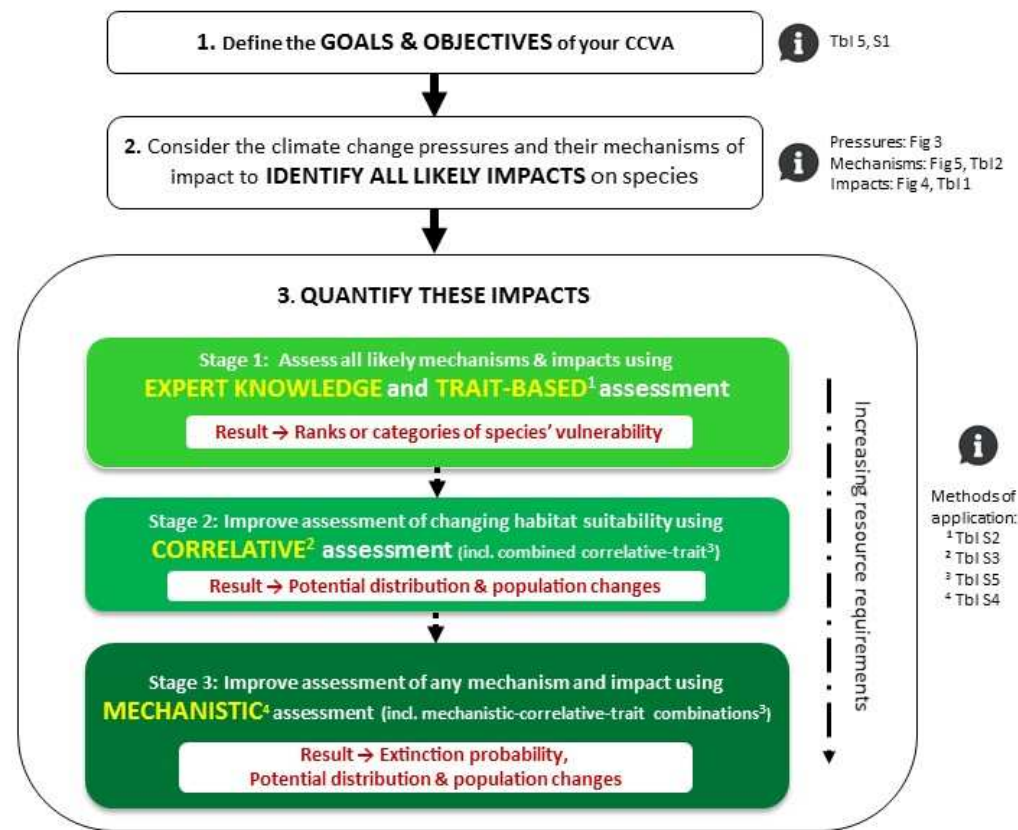
333   **Step 1: Define your goal and objectives**

334   A well-defined *goal* explains why a CCVA is being undertaken, who the audience is and which

335   decisions are intended to be influenced (Stein *et al*., 2012; Foden & Young, 2016). CCVAs can be

336   carried out, for example: to determine the degree of vulnerability to climate change of one or more

337   species in a region or across their entire ranges; to provide input into a specific adaptation planning

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338   process; to inform academic research (such as to generate input into a demographic model); or as an
339   educational exercise to provide the basis for teaching about how climate change might influence
340   species of interest. Identifying the audience, whether it be policymakers, land/resource managers,
341   scientists or the public, will inform the level of complexity needed for the analyses and the strategy
342   for communicating the results. If a CCVA aims to influence management practices, then
343   understanding the planning and management context for the species to be assessed will allow the
344   crafting of CCVA objectives and outputs to maximise their impact on those management processes,
345   with correspondingly greater benefits for the conservation of the species.

346   *Objectives* describe the one or more specific action steps needed to achieve your CCVA goal. CCVA
347   objectives can be grouped into five categories. Those are to identify, for specified taxonomic groups,
348   regions and time frames: (A) **which** species are most vulnerable; (B) **how vulnerable** species are (i.e.,
349   the magnitude of vulnerability); (C) **why** species are vulnerable; (D) **where** species are vulnerable;
350   and/or (E) **when** species become vulnerable. Further, some CCVAs include an objective to identify
351   data gaps. Table 5 summarises a framework for describing the objectives of a CCVA in clear and
352   certain terms, and Supplementary Table 1 provides examples of their use, including in the contexts
353   of a focus on taxonomic groups, single sites and larger extents.

354

355   *Table 5. Checklist to aid identification of clear, quantitative objectives.*

Select an **objective** category:						
	Which?	How much?	Why?	Where?	When?	What's missing?
Select a **taxonomic** focus (for example):						
	Subpopulation		Species	Higher taxonomic group	Multiple higher taxonomic groups	
Select a **spatial** focus:						
	Single site	Network of sites	Range of a subpopulation	Entire range of taxon/taxonomic group	Politically-defined geographical area (e.g. national, continental, global etc.)	
Select a **time frame** (for example):						
	Present	5 years		20 years	50 years	100 years

356

357   The *taxonomic focus* of a CCVA is typically on species, sub-species, metapopulations or
358   subpopulations, or on a group of species sympatric to an area of interest. An assessment's *spatial*
359   *focus* may be a single site or a network of sites (e.g. protected or other discrete areas), a political or
360   administrative unit, such as a province or a nation state, a larger spatial unit, such as a sub-continent
361   or continent, or a taxon's overall range. *Time frames* of assessments are most effectively shaped by
362   a combination of the needs of the intended audience (e.g. a planning horizon for site managers),
363   focal species' generation lengths and the intervals for which climate projections are more readily
364   available (e.g. 2016–2035, 2046–2065, 2081–2100 and 2181–2200 in the case of IPCC 2013 outputs).

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365

Step 2: Consider the climate change pressures and their mechanisms of impact to identify all likely climate change impacts

This step involves systematically considering the ways in which climate change can affect a focal species and identifying those that could pose a threat to one or more populations. The desired outcome is: a list of the *pressures* to which the focal species is likely to be exposed (Figure 3); the *mechanisms* through which these may impact the species (Figure 5, Table 2); and the *likely impacts* at species level, as mediated through potential impacts at individual and subpopulation levels (Figure 4, Table 1). Recording these in a logic flow format may be helpful.

Consultation with experts and literature is particularly important for this step, and gaining background knowledge of focal species, habitat(s), region(s) and climate is strongly advised. Assessors should consider the full range of climate change pressures, including abiotic, biological and human response pressures, as well as the role of interactions between climate change and other pressures (e.g. habitat loss, fragmentation) (Mantyka-Pringle *et al*., 2014). Where previous research has provided evidence that changes in particular climatic variables impact upon the focal species, or more generally upon members of the higher taxonomic group to which it belongs, this will help to inform the choice of climatic variables to use in the CCVA (see Step 3 and 'Selecting and using CCVA input data'). Topics to explore for focal species are a) ecology, distribution (including climate determinates), life history and threat status; b) documented and/or likely pressures; c) documented and/or likely mechanisms of impacts; and d) climate change impacts that may already have been observed.

It is also valuable to explore whether CCVAs have already have been conducted for the species. Examples of possible sources of existing CCVAs are shown in Supplementary Table 2. Assessors may subsequently choose to carry out assessments themselves, or to use those of others. In either case, evaluating assessment quality, including input data, is essential before making use of the results. Foden *et al*. (2016) and sections below covering selecting CCVA approaches, methods and input data provide guidance for evaluating their reliability and suitability for meeting CCVA goals and objectives.

Step 3: Quantify the impacts

In this step, the likely climate change mechanisms and their impacts identified in Step 2 are quantified according to three stages of increasing complexity, data and resource requirements, and applicability of resulting vulnerability metrics (Figure 6); each may help to inform the choice of focal mechanisms and impacts for subsequent stages. Assessors' choices of which stage(s) to complete typically include consideration of a) which deliver the vulnerability metrics needed to meet their CCVA objectives, and b) which they have sufficient resources (e.g. data, expertise, time) to apply. Where no alignment can be reached between these two considerations, assessors may consider revisiting objectives and/or mobilising additional resources. The three stages of complexity

21

406 correspond approximately with predominant CCVA approaches, namely *trait-based*, *correlative* and
407 *mechanistic approaches,* while the *combined approach* is applicable to stages two and three. We
408 outline each approach, discussing its strengths and limitations, methods of application, examples of
409 use and the vulnerability metrics it delivers. More detailed discussions can be found in Pacifici *et al.*
410 (2015).
411
412 In all cases, we recommend beginning with an expert-based assessment. This involves examining the
413 range of likely impact mechanisms in relatively non-technical and non-statistically intensive ways,
414 with the aim of categorising and potentially prioritising mechanisms according to their likely impacts
415 on focal species. At the most basic level, this involves considering species' exposure to climate
416 change pressures and, using available knowledge of the species' sensitivity and adaptive capacity to
417 estimate the likely relative or absolute magnitude of the impacts on the species. Red List
418 assessments may provide valuable information for such assessments because they help to identify
419 species with demographic and/or behavioural characteristics that increase their sensitivity; they also
420 identify other pressures faced by species that may be exacerbated by climate change.
421 Notwithstanding their limitations, expert-based assessments provide a valuable foundation for
422 identifying factors and mechanisms to focus on in subsequent stages.
423
424 *Trait-based approach*
425 This approach draws on the growing knowledge-base on associations between biological traits and
426 climate change impacts (e.g. Cardillo *et al.*, 2008; Murray *et al.*, 2009; Thaxter *et al.*, 2010; Angert *et*
427 *al.*, 2011; Chessman, 2013; Newbold *et al.*, 2013; Pearson *et al.*, 2014; Estrada *et al.*, 2015), and
428 makes use of a range of biological and life history information to score or rank species' probable
429 sensitivity and adaptive capacity to climate change. These are often combined with assessments of
430 exposure (e.g. Williams *et al.*, 2008; Young *et al.*, 2012; Foden *et al.*, 2013b; Smith *et al.*, 2016).
431 While in the strictest sense, 'traits' refer to the characteristics of an individual (Violle *et al.*, 2007), in
432 the context of CCVA of species the term is generally used more loosely to refer to a broad range of
433 species-level characteristics, examples of which are shown in Table 6 . Data relating to these traits
434 may be qualitative, categorical or quantitative; categories must be ranked according to risk, whilst
435 where trait data are quantitative, thresholds must be defined to determine risk categories. Trait-
436 level scores or ranks are then combined qualitatively or semi-quantitatively to assign species into
437 categories of vulnerability. We categorise methods for applying the trait-based approach according
438 to the ways in which their scores are developed (i.e. Qualitative vs. Semi-Qualitative) and describe
439 available tools, data requirements and examples (Supplementary Table 3). Trait-based approaches
440 may include the outputs of correlative and mechanistic approaches (e.g. Küster *et al.*, 2011; Young *et*
441 *al.*, 2012; Pompe *et al.*, 2014) or be included in other approaches (e.g. Garcia *et al.*, 2014a); we
442 discuss these further under the 'Combined approach'.
443
444 Because the trait-based approach requires ecological knowledge without strong modelling or
445 statistical expertise, and because it facilitates assessment of large numbers of species relatively
446 rapidly (Pacifici *et al.*, 2015; Foden & Young, 2016), it has been adopted by many conservation

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447 organizations. Limitations of the approach include the high degree of uncertainty about the links
448 between species' traits and climate change impact, as well as gaps in the availability of species-level
449 data for desired traits. Quantifying thresholds for high vs. low vulnerability for each trait is also
450 challenging, resulting in thresholds that are often arbitrary and relative (Thomas *et al.*, 2011; Foden
451 *et al.*, 2013; Pacifici *et al.*, 2015). Approaches for combining trait scores, discussed in detail in
452 Huntley *et al.* (2016), also remain challenging and typically produce categorical outputs. A study
453 comparing observed population trends in British birds and butterflies with CCVA results showed
454 poor predictive ability by trait-based assessments (Wheatley *et al.*, 2017); further validation and
455 method development are necessary. However, trait-based CCVAs remain valuable for exploring
456 species' sensitivity and adaptive capacity to climate change, as well as for understanding the relative
457 roles that potential impact mechanisms may have on the extent and nature of species' vulnerability
458 to climate change.
459

460 *Table 6. Examples of traits considered in four CCVAs (adapted from Willis et al. (2015) and Huntley et*
461 *al. (2016)).*

	Graham *et al.* (2011)	Gardali *et al.* (2012)	Garnett *et al.* (2013)	Foden *et al.* (2013)	Young *et al.* (2012)
Degree of exposure to climate change		X	X	X	X
Breadth of environmental / climate tolerance(s)		X	X	X	X
Phenological dependence upon seasonal climate trigger(s)				X	X
Degree of habitat specialisation	X	X	X	X	X
Degree of dietary (animals) and pollinator (plants) specialisation	X		X		X
Degree of specialisation of inter-specific interactions				X	X
Dispersal capacity		X		X	X
Migratory status		X			
Capacity for rapid genetic adaptation				X	X
Plant reproductive mode					X
Reproductive/recruitment capacity	X		X	X	
Rarity			X	X	
Degree of exposure to other pressures					
Body size	X				
Brain size			X		

462
463

464 *Correlative approach*

465 Perhaps better termed the 'Climate-matching approach', this includes 'niche-based', 'climate
466 envelope' and 'species distribution modelling'. Correlative assessment depends upon fitting models
467 that describe the correlation between each focal species' distribution, usually in the recent past (i.e.
468 the late twentieth century), and the contemporary climate. The fitted model aims to reflect the

23

469 species' realised niche (Hutchinson, 1957) during the period to which the distribution and climate
470 data relate and can be used to infer its climate requirements or ecological tolerances. Correlative
471 assessments can be used to identify those geographical areas where climate is likely to be suitable
472 for the species under any projection of potential future climate (Pearson & Dawson, 2003; Beale *et*
473 *al.*, 2008), and hence to estimate its potential distribution under those climate conditions. A species'
474 climate change vulnerability is inferred from differences between its recent distribution and its
475 predicted potential future distribution in terms of extent, location and sometimes degree of
476 fragmentation (e.g. Garcia *et al.*, 2014a), and also their degree of overlap (Huntley *et al.*, 2007).
477 Correlative approaches have been used to predict species' potential distribution changes at various
478 spatial scales (Pacifici *et al.*, 2015), and have been widely applied to assess climate change
479 vulnerability of plants (Midgley *et al.*, 2002; Thuiller *et al.*, 2005; Fitzpatrick *et al.*, 2008),
480 invertebrates (Harrison *et al.*, 2006; Settele *et al.*, 2008; Heikkinen *et al.*, 2010; Sánchez-Fernández
481 *et al.*, 2011) and vertebrates, including birds (Gregory *et al.*, 2009; Hole *et al.*, 2011; Garcia *et al.*,
482 2012), mammals (Hughes *et al.*, 2012; Songer *et al.*, 2012; Visconti *et al.*, 2015), amphibians (Lawler
483 *et al.*, 2009; Carvalho *et al.*, 2011) and fishes (Jeschke & Strayer, 2008; Yu *et al.*, 2013). We
484 categorise methods for applying the correlative approach as climate envelope, regression-based,
485 machine learning and Bayesian, and describe available tools, data requirements and examples of
486 their application (Supplementary Table 4).
487
488 Correlative assessments are very widely used, probably because methods of application are
489 relatively rapid and cost-effective, occurrence data required are easily available for a large number
490 of taxa, and due to their applicability for spatial conservation planning (e.g. Hannah *et al.*, 2002;
491 Araujo *et al.*, 2004; Phillips *et al.*, 2008; Araújo *et al.*, 2011). Choice of modelling technique is one of
492 the major sources of uncertainty in correlative models (Diniz-Filho *et al.*, 2009; Garcia *et al.*, 2012)
493 but valuable guidance on using and understanding correlative models is available, including from
494 (Pearson, 2007; Franklin, 2009; Peterson *et al.*, 2011; Anderson, 2012, 2013). Shortcomings of
495 correlative CCVAs have been widely discussed (e.g. Pearson & Dawson, (2003b), Hijmans & Graham
496 (2006), Hannah *et al.*, (2007), Araújo & Peterson (2012) and Pacifici *et al.*, (2015)); their assumption
497 that species' distributions are in equilibrium with the prevailing climate can prove problematic in
498 cases where a species' contemporary distribution reflects the outcome of recent or historical
499 pressures (e.g. habitat loss, persecution) or natural dispersal barriers that have excluded the species
500 from areas of suitable climate (Guisan & Thuiller, 2005). Other challenges include poor performance
501 for species with few records (see section below on 'Species that pose particular CCVA challenges'),
502 failure to account for local adaptation, and difficulty in projecting suitability for novel climatic
503 conditions (i.e. outside the climatic range of the training data).
504
505 When validated using species' observed responses to recent climate changes, however, correlative
506 CCVAs have been shown to perform well in predicting species' population increases/decreases in
507 many cases (Green *et al.*, 2008; Gregory *et al.*, 2009; Stephens *et al.*, 2016) and to have a fair ability
508 to predict distribution changes (e.g. Chen *et al.*, 2011; Dobrowski *et al.*, 2011; Morelli *et al.*, 2012;
509 Smith, 2013). The range of potential impact mechanisms may be increased, for example, by
510 incorporating variables such as inter-species interactions (e.g. Schweiger *et al.*, 2008, 2012), the

24

511 availability of nesting sites (e.g. Heikkinen *et al.*, 2007) and habitat shifts (e.g. Thuiller *et al.*, 2006a)
512 along with climate variables in models. Further advances are being made by combining correlative
513 and trait-based approaches, including by incorporating estimates of dispersal ability (e.g. Warren *et*
514 *al.*, 2013) and sensitivity and adaptive capacity (e.g. Garcia *et al.*, 2014a) into projections of species'
515 range shifts (see 'Combined approach' and 'Improving CCVA methodology' below).
516

517 *Inferring distribution changes from model projections*
518

519 Most correlative models output continuous values of 'suitability' or probability of occurrence of a
520 species for each grid cell, generally requiring assessors to select a threshold value separating species
521 'presence' from 'absence' in order to estimate potential changes in the species' distribution.
522 Threshold values are typically determined as those which optimise model goodness-of-fit. However,
523 as Liu *et al.* (2005, 2013) showed, different measures of goodness-of-fit can give very different
524 threshold values, with the True Skill Statistic (Allouche *et al*., 2006) emerging as the most robust
525 measure for this purpose. However, since different thresholds can yield dramatically different
526 conclusions about whether a species' distribution will decrease or expand under climate change
527 (Nenzén & Araújo, 2011), we recommend carefully experimenting with alternative threshold rules
528 with consideration as to whether optimistic or pessimistic outcomes are more appropriate for the
529 analysis. A complement or alternative to thresholding is to use the raw suitability values to assess
530 whether environmental conditions improve or degrade for the species (e.g. Still *et al.*, 2015), i.e.
531 how the 'quality' of the potential area of distribution changes.
532

533 *Inferring population changes from distribution changes*
534

535 Changes in distribution extent are unlikely to be linearly related to population changes because: (a)
536 individuals are rarely evenly spread throughout a species' overall distribution; (b) suitable habitat
537 patches in areas newly climatically suitable may not be large enough to support viable
538 subpopulations; and (c) dispersal limitations may prevent the species from colonising areas that
539 become newly climatically suitable. These factors are species-specific and must therefore be
540 considered separately for each focal species' CCVA. In the context of IUCN Red Listing, in the
541 absence of more specific information, it is allowable to infer a linear relationship between
542 population and distribution changes (although this should be explicitly stated). Suitability values
543 provide a basis for improving upon such an assumption; even without any change in distribution
544 extent, a decrease in mean suitability indicates a likely population decline. Where abundance data
545 (or a proxy for abundance, e.g. recording rate) are available, these may be used to model the
546 relationship between abundance and bioclimatic variables, hence enabling projections of future
547 abundance patterns which are then more closely linked to measures of future conservation status
548 and extinction risk (e.g. Huntley *et al.*, 2012; Renwick *et al.*, 2012; Johnston *et al.*, 2013; Massimino
549 *et al.*, 2017).
550
551

25

Mechanistic approach

Mechanistic assessments use process-based simulation models to quantify climate change impacts, and explicitly incorporate focal mechanisms (Morin & Thuiller, 2009), thereby allowing projection under novel climate conditions. One of two sub-types (Supplementary Table 5), *mechanistic niche* models, project species' future ranges using estimates of species' physiological tolerances, typically from field or laboratory observations (e.g. Jenouvrier *et al.*, 2009; Radchuk *et al.*, 2013; Overgaard *et al.*, 2014) or energy balance equations (e.g. Molnár *et al.*, 2010; Huey *et al.*, 2012; Kearney & Porter, 2009). Because they estimate species' fundamental niches they may perform poorly in predicting realised niches when species interactions are important, especially when physiological tolerances are measured in the laboratory. Secondly, *demographic* models project changes in abundance, usually through simulating climate change impacts on individuals, subpopulations, or species (e.g. Stanton, 2014; Aiello-Lammens *et al.*, 2015; Heinrichs *et al.*, 2016; Naveda-Rodríguez *et al.*, 2016); they can therefore be used to assess extinction risk (e.g. Keith *et al.*, 2008; Brook *et al.*, 2009; Pearson *et al.*, 2014). However, such models are very data intensive, requiring knowledge of the relationships between a series of demographic parameters (e.g. adult survival, juvenile survival, fecundity) and relevant climate variables. Supplementary Table 5 provides a further classification of mechanistic models, as well as examples of their use.

Mechanistic CCVAs can include a broad range of climate change impact mechanisms, including changes in resource availability (e.g. Mantyka-Pringle *et al.*, 2014; Martin *et al.*, 2015), habitat suitability (e.g. Aiello-Lammens *et al.*, 2011; Forrest *et al.*, 2012), and inter-specific interactions (e.g. Urban *et al.*, 2012; Fordham *et al.*, 2013). They can also accommodate interaction effects of climate change and other pressures (e.g. land-use change; Mantyka-Pringle *et al.* (2014, 2016)), as well as direct mortality in specific but different subpopulations and age classes. Morphological and demographic factors, genetic adaptation and phenotypic plasticity may also be included (e.g. Chevin *et al.*, 2010; Huey *et al.*, 2012). Use of such species trait data in the mechanistic approach is distinguished from that of the Trait-based approach, since the latter relies on assessors' *a priori* assumptions of the links between traits and species' vulnerability, while the Mechanistic approach integrates traits into process-based empirical predictions. However, their often intensive requirements for knowledge and data on species and their systems (Morin & Thuiller, 2009), and hence their relative costliness (Kearney & Porter, 2009; Chevin *et al.*, 2010), have significantly limited their application to date and are likely to do so for the foreseeable future.

Combined approach

Combining CCVA approaches such that they draw on the strengths of component approaches provides a valuable opportunity to improve CCVA of species (Willis *et al.*, 2015). The trait-based approach, for example, can draw on correlative assessments to estimate range shift predictions and to understand the climatic variables associated with the species' historical ranges (i.e. a trait-correlative approach)(e.g. Young *et al.*, 2012; Smith *et al.*, 2016). The Correlative approach can draw on the trait-based approach by using dispersal distances (e.g. Schloss *et al.*, 2012; Warren *et al.*, 2013, 2018; Visconti *et al.*, 2015), and measures of species' sensitivity and adaptive capacity (e.g.

26

593   Garcia *et al.*, 2014a) to improve range shift predictions (i.e. a correlative-trait approach). Correlative

594   and mechanistic approaches may be used in combination to enable inclusion of a range of

595   potentially important variables for predicting the suitability of potential future range, including

596   metapopulation dynamics and environmental processes such as sea level rise, fires and stochasticity

597   (e.g. Keith *et al.*, 2008; Anderson *et al.*, 2009; Midgley *et al.*, 2010; Fordham *et al.*, 2012), as well as

598   inter-species interactions (e.g. Harris *et al.*, 2012; Fordham *et al.*, 2013) (i.e. a correlative-

599   mechanistic approach). Finally, all three approaches may be combined in Criteria-based assessments

600   in which species are classified into categories of risk based on the information from correlative

601   and/or mechanistic assessments, species trait data and observed species changes (e.g. Thomas *et*

602   *al.*, 2011) (i.e. a correlative-mechanistic-trait Approach). We provide further details of combined

603   approaches, including data requirements, available tools and examples of their application

604   (Supplementary Table 6), and discuss their potential for advancing CCVA of species under 'Future

605   directions'.

606

607

608   **SELECTING AND USING CCVA INPUT DATA**

609   A growing body of data and resources for CCVA of species is now available online but selecting and

610   using these appropriately can be challenging (Wade *et al.*, 2017). We discuss these below and

611   provide summaries of CCVA resources in Supplementary Tables 7 and 8; a synthesis of the input data

612   requirements for trait-based, correlative and mechanistic CCVA approaches is also provided

613   (Supplementary Table 9). An important first consideration in setting the parameters of the

614   assessment is defining the spatial extent and resolution of the CCVA. The *spatial extent* of a CCVA is

615   the total area under consideration; this may be specified by the CCVA objective and/or encompass

616   the distribution range of focal species. Two important considerations help to avoid over-estimating

617   vulnerability when predicting areas of suitable climate in the future. Firstly, for species-focused

618   CCVA objectives, including the full distribution range is important for estimating the species' full

619   niche breadths. Secondly, it is important to include sufficient area around the current range such

620   that the spatial extent includes all areas that could feasibly become suitable for the species in the

621   future time frames considered. Considering an excessively large area, however, will inflate model

622   accuracy and pick up broad-scale rather than finer-scale differences in suitability (e.g. Anderson &

623   Raza, 2010).

624   *Spatial resolution* or grain is relevant when CCVA is to be carried out using a modelling approach that

625   requires gridded data and refers to the grid cells' area or linear dimensions. Ideally, the spatial grid

626   size should be ecologically relevant for the study species (i.e. reflecting relevant ecological

627   processes) and capture the way individuals perceive the environment (Potter *et al.*, 2013). In

628   practice the grid size used in most studies is orders of magnitude larger and is often be determined

629   by the resolution of data available, since the essential dataset with the coarsest resolution generally

630   determines the limit to which grain size can be reduced. For example, whilst elevation data may be

631   available on a 50m grid (i.e. 50m x 50m), if species' distribution data are recorded for a 1km grid, the

632   latter is the finest grain size possible for most analyses (Foden & Young, 2016). Finer resolutions may

633   be necessary to represent areas of higher spatial heterogeneity (e.g. topographically complex or

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634   with varying land-surface properties), but the associated increase in computational demands as
635   grain size reduces typically poses a practical limit. At resolutions >20km, species' abundance and
636   distributions can generally be explained by bioclimatic variables alone (Luoto *et al.*, 2007), but at
637   finer scales variables related to habitat suitability, land use and management become important,
638   and below 1 km microclimate becomes dominant. In the latter case, microclimate influences should
639   be explored taking into account factors such as slope, aspect, vegetation and shading by adjacent
640   areas at higher elevation (see e.g. Bennie *et al.*, 2008, 2013; Gillingham *et al.*, 2012; Hodgson *et al.*,
641   2015). At almost all grain sizes relevant to CCVAs important issues that arise with respect to
642   downscaling climate model outputs should be considered (Baker *et al.*, 2017).
643
644   **Species data**

645   *Distributions*

646   For methods that rely on occurrence or locality records to characterise species' bioclimatic
647   tolerances (i.e. correlative modelling approaches), using data of good quality is particularly
648   important. Ideal sources include surveys or atlases, and well-validated specimen and citizen science
649   records. Data from large distribution databases (Supplementary Table 7) provide a convenient
650   source of data but must be carefully reviewed for accuracy. Where available, data on species'
651   abundances (or based on abundance proxies such as reporting rate) are especially valuable. Expert-
652   developed range polygons may be used when they are based on first-hand knowledge of current
653   species occurrence or where gridded data or point records are unavailable, but they are likely to
654   have a higher incidence of false presences (commission errors) especially if patchiness in the species'
655   distribution within polygons is not accounted for.
656
657   False presences also arise from species misidentification or taxonomic uncertainty, incorrect locality
658   recording or data entry error, and can lead to overestimation of species' environmental niches. The
659   most common cause of uncertainty, however, is false absences (omission errors). These typically
660   arise from spatial differences in sampling effort (e.g. low sampling effort away from roads, in
661   inaccessible areas, or in countries with limited resources to survey biodiversity), differences in
662   detectability (e.g. fewer records of cryptic species) or in level of interest/charisma (e.g.
663   disproportionate number of records for charismatic species). Some datasets provide data from
664   which detection probability can be estimated (e.g. Southern African Bird Atlas Project (Harrison *et
665   al.*, 1997) Breeding Bird Surveys (Massimino *et al.*, 2017) or on areas where the species was sought
666   and not found (e.g. European Bird Census Council Atlas (Hagemeijer & Blair, 1997). For correlative
667   models, Guillera-Arroita *et al.* (2015) provide guidance on how the type of distribution data (and
668   associated sampling bias) determines the quantity that is estimated by the models. Various
669   approaches have been proposed to address spatial biases in species' presence data. Phillips *et al.*,
670   (2009) developed models that use all records of presence for members of a group of species to
671   generate a background sample of pseudo-absences for the focal species that have the same spatial
672   bias as the collective presence records. Other approaches include Bayesian approaches (Manceur &
673   Kühn, 2014; Rocchini *et al.*, 2017), subsampling in geographic space (Aiello-Lammens *et al.*, 2015) or

28

674   in environmental space (Varela *et al.*, 2014), and weighting presences by the inverse of their density
675   (Stolar & Nielsen, 2015).

676   *Trait and life history information*

677   Databases containing such information are increasingly available (Supplementary Table 7) but for
678   the many taxa with few data available, data can be collected based on expert knowledge or inferred
679   from similar species. There has also been some progress towards imputing unknown trait data based
680   on probabilistic models (Penone *et al.*, 2014; Schrodt *et al.*, 2015). Recognition of the importance of
681   understanding, recording and using trait variability, in addition to trait means, is also emerging
682   (Cordlandwehr *et al.*, 2013). Since understanding of climate change impact mechanisms and the
683   extent to which they are associated with particular traits will increase as impacts become
684   increasingly apparent and more data become available, it is important to document both the
685   rationales for trait choices, as well as desired traits or data that could be included at later stages.
686   Similarly, since selection of thresholds of climate change vulnerability remains challenging and often
687   subjective, recording thresholds used and the rationales for determining them is essential.
688

689   **Climate data**

690   The decision about which climate projection(s) to use is one of the most important in CCVA (Snover
691   *et al.*, 2013). It is influenced by three key questions: *(i)* Which bioclimatic variables should be used?
692   (ii) Which General Circulation Models are appropriate? and *(iii) W*hich Representative Concentration
693   Pathways are relevant? We provide a summary of data resources for future and palaeoclimates
694   (Supplementary Table 7) as well as for the climates of 'present' or recent past (Supplementary Table
695   8). To ensure that CCVAs are transparent and reproducible, climate data used should be reported;
696   Morueta-Holme *et al*. (2018) propose best-practices for this purpose.
697

698   *Bioclimatic variables*
699

700   Many CCVA studies have used simple climate variables that, whilst giving statistically significant
701   models, very often have no understood mechanistic relationship with the focal species' performance
702   and/or survival. For correlative approaches, even where models have a high goodness-of-fit and/or
703   statistical significance, they may only reflect correlations between mechanistically relevant variables
704   and those used in the model. As a result, such correlations may not persist as one moves in space
705   from one climate regime to another (see e.g. Huntley, 2012; Dormann *et al.*, 2013; Huntley *et al.*,
706   2014) or across time as climate patterns change. For these reasons, it is extremely important to use,
707   as far as possible, only variables for which a plausible mechanistic role can be identified. As a general
708   rule, no more than one bioclimatic variable should be used for every five species occurrence records
709   or 'presence' grid cells (IUCN SSC Standards and Petitions Subcommittee, 2017). This avoids the risk
710   of model 'over-fitting' which occurs where highly complex models begin to describe or 'fit' random
711   error or noise, instead of a meaningful relationship between variables. Transferability of over-fitted
712   models in time or space becomes problematic.

29

713   Autecological studies identifying precise bioclimatic variables that affect a particular species'
714   performance or survival, and their mechanisms of action, are rare (e.g. Pigott & Huntley, 1981).
715   However, general biological knowledge accumulated for a variety of taxonomic groups and climate
716   regions, assessments of bioclimatic variable performance (e.g. Barbet-Massin & Jetz, 2014) and
717   previous published models provide a basis for an informed choice of bioclimatic variables for most
718   species. Mean annual temperature or precipitation are unlikely ever to be mechanistically important
719   (Bateman *et al.*, 2012; Huntley, 2012; Platts *et al.*, 2013) but coldest and/or warmest month means
720   or annual extremes and annual thermal sums above or below relevant thresholds, for example, have
721   well-understood mechanistic roles for a wide range of taxonomic groups. For higher plants, the
722   balance between precipitation and evaporation is mechanistically relevant, while members of other
723   taxonomic groups may be greatly influenced by the distribution of precipitation through the year.
724   Other taxon-specific measures relating to particular periods of high sensitivity to weather conditions,
725   such as the breeding season (Pearce-Higgins *et al.*, 2015a) may also be considered.
726
727   Regionally, for tropical species, relevant bioclimatic variables are likely to include a combination of
728   coldest and warmest month mean temperatures, annual ratio of actual to potential
729   evapotranspiration, the intensity of the dry/wet season, and measures of rainfall bimodality (i.e.,
730   two rainy seasons in a year). For temperate species, the best default bioclimatic variables are likely
731   to include the coldest month mean temperature, annual thermal sum above 5°C, and the annual
732   ratio of actual to potential evapotranspiration. For some cool temperate species that have a 'chilling'
733   requirement, a measure of the length of the period with temperatures below a threshold (e.g. 0°C),
734   or the (negative) annual thermal sum below 0°C can be an important additional variable, as well as
735   snow water equivalent (SWE).
736
737   *General Circulation Models (GCMs).* GCMs are computationally intensive mathematical models of
738   atmosphere and ocean processes that are used to generate weather forecasts and climate change
739   projections. GCM outputs differ due to dissimilarities in the ways that models simplify and simulate
740   *extremely* complex systems, as well as due to knowledge-gaps in climate science. No GCM perfectly
741   reproduces all of the features of the global climate system, so use several models to understand the
742   uncertainties in projections is essential. Fordham *et al.* (2011, 2012) offers some tools for model
743   selection, ensemble building based on model skill, and downscaling. Model inclusion by the IPCC in a
744   recent report (IPCC, 2013) conveys legitimacy, and those selected should reflect the range of
745   uncertainty amongst models by including those that are relatively 'warm', 'cool', 'wet', and 'dry', as
746   well as those whose mean temperature and precipitation projections are near the mean of all
747   models. Models that perform 'best' in the geographical region of interest should be favoured (Baker
748   *et al.*, 2015). Where possible, use of observed climate data to assess model performance under past
749   conditions in CCVA focal areas is also valuable. The IPCC's Data Distribution Centre is a portal for a
750   broad range of GCM outputs.

751   Projections from the individual models selected, collectively referred to as the model 'ensemble',
752   may be averaged to produce a single projection, with the degree of agreement between projections
753   represented by a measure of 'spread' such as the standard deviation or coefficient of variation (for
754   details and caveats of model averaging, see Dormann *et al.* (2018)). While this is often carried out in

30

755   other contexts, for CCVA this is inadvisable because it provides little insight into the uncertainty of
756   CCVA outputs. Conducting individual assessments using projections from several (at least three)
757   individual models is preferable to a single assessment applied to one model ensemble. Additionally,
758   since different models may generate qualitatively different circulation patterns, averaging them
759   could also result in an ensemble mean projection that is mechanistically unrealistic or physically
760   impossible, or that disguises year-to-year variations that may be important drivers of vulnerability.
761
762   Where a CCVA's spatial extent is relatively limited, and particularly in areas of complex topography,
763   projections using Regional Climate Models (RCMs (Morales *et al.*, 2007)) are generally more accurate
764   than GCM projections downscaled using change factors or statistical downscaling, because RCMs
765   operate mechanistically on horizontal resolutions of tens rather than hundreds of kilometres. The
766   island of Madagascar, for example, is spanned by only approximately 15 grid cells at a typical GCM
767   resolution, but by over 300 RCM cells (55 km in size). However, it is essential to ensure that the
768   GCM-derived boundary conditions used by the RCM simulation are from an appropriate GCM
769   simulation. The Coordinated Regional Climate Downscaling Experiment (CORDEX) provides a series
770   of regional datasets derived from RCM simulations at continental scale, with a grain size of 0.11 to
771   0.44 decimal degrees (~12 to 49 km at the equator) depending on the model and continent, whilst
772   the Hadley Centre PRECIS RCM can be run using either this grain size or a 25km grid (Jones *et al.*,
773   2004). Where possible, use of the most appropriate regional models that have been shown to
774   provide good predictive performance for the area / variables of interest is advisable (Baker *et al.*,
775   2017). Even regional models, however, are unable to account for fine-scale climate variability across
776   regions with high relief. A subsequent, non-mechanistic, downscaling step may therefore be
777   desirable to recover finer-scale spatial variation at sub-RCM grid scales; the change factor method,
778   for example, involves combining anomalies between modelled current and projected climate
779   variables with those from observed climate datasets at finer scales (see Foden & Young, 2016).
780
781   *Greenhouse Gas Trajectories and Emissions Scenarios*
782
783   Greenhouse gas trajectories aim to capture the uncertainty in future climate due to different future
784   anthropogenic emissions. The IPCC's Fifth Assessment Report (IPCC, 2014) includes four
785   Representative Concentration Pathways (RCPs) or trajectories: RCP 2.6, RCP 4.5, RCP 6 and RCP 8.5
786   (the radiative forcing in $W.m^{-2}$ determines the number succeeding RCP), which supersede the SRES
787   scenarios used by the IPCC's third (2001) and fourth (2007) assessments. Selecting trajectories
788   typically involves identifying a broad range of plausible possible futures and may include adoption of
789   the precautionary principle. In support of the latter, evidence from the past 25 years is that
790   emissions have continued more or less along the worst-case trajectory (i.e. 'business-as-usual')
791   considered plausible by the IPCC in 1990 (Raupach *et al.*, 2007). In addition, improvements in climate
792   models over the same period have not reduced the magnitude of disparities between changes
793   projected by different models and under different emissions scenarios, nor have they resulted in any
794   substantial change in the magnitude of projected potential climate changes. If the precautionary
795   principle is adopted, then RCP8.5 is recommended.

31

796   To apply the 'plausible range of futures' approach, we suggest using either two or all four RCPs to
797   represent the overall range of plausible uncertainty about future emissions. Selecting an odd
798   number of RCPs is not recommended, because readers of the assessment may be inclined to
799   interpret central values as most likely, and thus underestimate the uncertainties involved. Because
800   achieving RCP2.6 is unlikely given our current trajectory, a common choice is to select RCP4.5 and
801   RCP8.5 as the low and high emissions scenarios respectively, and indeed regional climate centres
802   sometimes prioritise simulations with these forcings. However, RCP2.6 matches most closely to the
803   ambition of 'Holding the increase in the global average temperature to well below 2°C above pre-
804   industrial levels and to pursue efforts to limit the temperature increase to 1.5°C' agreed by parties of
805   the UNFCCC in Paris, 2015. Considering also the recent advances in carbon capture technologies
806   (Keith *et al.*, 2018), the option of including RCP2.6 as an optimistic (low emissions) scenario should
807   not be discounted (van Vuuren *et al.*, 2011). In contrast to working with climate models, it is
808   inappropriate to calculate any kind of ensemble mean of the CCVA results for two or more RCPs.
809   Instead, individual CCVAs should be made for each RCP in order to capture uncertainty in the CCVA
810   due to the unknown future radiative forcing.

811

Ecological data

813   Arguably the most important ecological pressure on many species from climate change, particularly
814   over multi-decadal time scales, is through shifts, degradation, and changes in the extent of areas
815   offering suitable habitat; unless these are considered in combination with climate suitability, CCVA
816   may be inaccurate. Ecological changes have already been observed in response to climate and
817   atmospheric carbon dioxide, for example as shrubs expand northward into the Arctic tundra boreal
818   forest (Swann *et al.*, 2010; Blok *et al.*, 2011; Hill & Henry, 2011), and African savannah grasslands are
819   transformed into woodlands (Bond & Midgley, 2012). When modelling species abundance, the
820   inclusion of such habitat variables is particularly important (e.g. Renwick *et al.*, 2012). Although land-
821   cover data for the 'present' (i.e., recent past) are widely available (Supplementary Table 7) and have
822   been used for projecting species' future ranges (e.g. Renwick *et al.*, 2012; Pearce-Higgins & Green,
823   2014; Massimino *et al.*, 2017), use of projections of future land cover (i.e. considering climate
824   change and other pressures) is, in principle, preferable. Some authors have begun to use Dynamic
825   Global Vegetation Models (Cramer *et al.*, 2001; Scheiter & Higgins, 2009; Scheiter *et al.*, 2013) to
826   estimate future vegetation changes (e.g. Thuiller *et al.*, 2006; Blanco *et al.*, 2014; Talluto *et al.*, 2016;
827   Case & Lawler, 2017). Pompe *et al.* (2008) combined scenarios of climate and land use changes up to
828   2080 based on three 'storylines', in order to model the future ranges of German plant species, while
829   Hannah *et al* (2013) considered future agricultural land-use changes in response to climate change.
830   However, such projections introduce a new level of uncertainty, being based upon a series of
831   alternative socio-economic projections themselves.

Data on human response pressures

833   Most current CCVA methods ignore the impacts of human responses to climate change on
834   biodiversity, even though these could match or exceed impacts arising directly from abiotic or biotic

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835 pressures (Turner *et al*., 2010, but see Young *et al*., 2012). Such responses include changing land use
836 (e.g. due to expansion of biofuel plantations, land abandonment, new agricultural demands as
837 people migrate), increased water abstraction and building hard infrastructure (e.g. sea walls, dams,
838 wind and solar energy installations) (Watson, 2014; Segan *et al*., 2015). The advent of Nature-based
839 Solutions (Kabisch *et al*., 2016; Nesshöver *et al*., 2017), however, introduces the likelihood that some
840 human responses will have positive impacts on species. Segan *et al*. (2015) found that the relative
841 vulnerabilities of Southern African bird species changed markedly when potential impacts of climate
842 change on human communities were considered (Supplementary Table 7 includes the resources
843 they used). Although human response pressures are difficult to predict, their inclusion is a priority
844 for future CCVA approaches (Maxwell *et al*., 2015).

845

846 **SPECIES THAT POSE PARTICULAR CCVA CHALLENGES**

847 Although CCVA has been widely applied across taxonomic groups (Pacifici *et al*., 2015), many species
848 are poorly assessed or frequently omitted due to insufficient occurrence, trait or physiological data.
849 We focus here on species that are omitted from assessments, but note that others such as long-
850 distance migrants may face concerning shortcomings in their assessments due to failure to explicitly
851 incorporate migratory connectivity (Small-Lorenz *et al*., 2013). With the exception of well-studied
852 taxonomic groups, incomplete species coverage in CCVA applications is common. Species omission
853 rates as high as 33% for African vertebrates (Garcia *et al*., 2012), 42% of 5,200 species across 17 taxa
854 in England, a relatively well-monitored and data-rich country (Pearce-Higgins *et al*., 2017) and 92%
855 for threatened sub-Saharan amphibians (Platts *et al*., 2014) mean that general conclusions about
856 species' vulnerability to climate change may be biased toward better-known species (Schwartz *et al*.,
857 2006; Platts *et al*., 2014). Challenges in the application of conventional CCVA methods arise for three
858 types of species in particular: those that are *poorly-known*, those with *naturally small ranges*, and
859 those with *ranges that have become smaller due to other anthropogenic pressures*. For these species
860 to be included in assessments, enhanced data to allow the use of conventional CCVA methods,
861 modified CCVA methods or alternative approaches are needed.

862 Efforts to fill data gaps and use conventional CCVA methods can rely on inferences from data for
863 related species (Foden *et al*., 2013), expert opinion (Murray *et al*., 2009; Martin *et al*., 2015), data
864 imputation techniques, or a combination of literature and targeted fieldwork (Williams *et al*., 2009).
865 Conventional CCVA methods can be modified to accommodate incomplete data. Correlative
866 modelling of poorly-known and small-range species can rely on simplified correlative techniques
867 (Hof *et al*., 2011; Platts *et al*., 2014), more complex techniques with adjusted parameters (Hof *et al*.,
868 2011), methods that account for potential biases in sampling effort (Beale *et al*., 2014), or consensus
869 building around several models based on a small number of predictors (Lomba *et al*., 2010). For
870 declined-range species, correlative models could overestimate climate change vulnerability if, for
871 example, warmer parts of the range have been lost for non-climatic reasons (e.g. deforestation at
872 low elevations); therefore, the extant range should be augmented with information on the historic
873 range whenever possible. Another modification to conventional CCVA methods is to redefine
874 taxonomic focus of the models, selecting either a resource used by the focal species that has

33

875   sufficient data (Delean *et al*., 2013), or a species assemblage that includes the focal species.

876   Assemblages can be defined with reference to community types (Ferrier & Guisan, 2006), biomes

877   (Midgley *et al*., 2003), or shared traits (Golicher *et al*., 2008; Vale & Brito, 2015) that are thought to

878   mediate species' responses to climate change. Caution is needed, however, in the use of such

879   approaches given the evidence from the Quaternary record of the individualistic responses of

880   species to past climate changes (e.g. Huntley, 1991; Graham *et al*., 1996) and the resulting

881   impermanence of species assemblages (e.g. Graham & Grimm, 1990; Huntley, 1996).

882   Alternative approaches make use of available data to draw inferences about species' vulnerability to

883   climate change (Table 7). When historical data on population and climate variability are available,

884   temporal analysis can be used to identify long-term trends in potential climate drivers of population

885   change and infer future population changes under projected climates (Pearce-Higgins *et al*., 2017).

886   When the information available is restricted to climate data, assessments can be based solely on the

887   exposure of geographical areas to climate changes. Analysis of multiple dimensions of climate

888   change, such as velocities of temperature change or the disappearance of specific climate

889   conditions, and associated threats and opportunities for species (Garcia *et al*., 2014b) can provide

890   indications of the likely vulnerability of species present in such areas (Ohlemuller *et al*., 2008; Garcia

891   *et al*., 2014a).

34

Table 7. Alternative approaches for carrying out CCVA in three challenging situations, namely for poorly-known species, those with naturally small ranges, and those with ranges that have become smaller due to anthropogenic threats (from Foden et al., 2016)

	Poorly-known species	Small-range species	Declined-range species (not climate related)
Conventional approaches			
Correlative models	Statistically problematic where occurrence records are insufficient	Statistically problematic due to insufficient occurrence records	Problematic since extant range cannot be used to infer environmental niche
Mechanistic models	Problematic where mechanistic information is insufficient	Applicable if mechanistic data available	Applicable if mechanistic data available
Trait-based models	Problematic where trait information is insufficient	Applicable if trait data available	Applicable if trait data available
Alternative approaches			
i. Fill data gaps	High priority; data addition or inference may render all conventional approaches applicable	Beneficial for correlative approaches if new data extend known distribution range. New trait data may render conventional trait-based and mechanistic approaches applicable	Additional data on extinct localities or range are advisable to complement extant occurrence records for correlative modelling (thus increasing environmental niche coverage). Additional trait data likely to render conventional trait-based and mechanistic approaches applicable
ii. Temporal analysis of population variability	Potentially the best solution, but problematic where time-series information is insufficient. May not fully capture impact mechanisms associated with long-term climatic change.	Potentially applicable, if robust time-series of inter-annual population variability are available. Underlying demographic processes should be carefully considered. May not fully capture impact mechanisms associated with long-term climatic change.	Potentially applicable, if robust time-series of inter-annual population variability are available. Underlying demographic processes should be carefully considered. May not fully capture impact mechanisms associated with long-term climatic change.
iii. Modified correlative	Potentially applicable; advantageous when	Potentially applicable, and advantageous	Potentially applicable, but important to

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techniques	species-level results are essential, although results will be less reliable	when species-level results are essential	ensure that predictors associated with decline are included in model or used to filter model projections
iv. Alternative taxonomic focus	Assessing assemblages of associated species is applicable when species-level results are not essential. This can be applied using conventional correlative and trait-based approaches	Apply correlative models to interacting species, particularly where closely coupled to the focal species (e.g., specialist resource species or close competitors). Assessing assemblages of associated species is applicable when species-level results are not essential; this can be applied using conventional correlative or trait-based approaches	As for 'small-range species'. Assessing assemblages is particularly relevant where they share a common reason for decline. Ensure that predictors associated with decline are included in model or used to filter model projections
v. Exposure assessment of geographic area	Potentially applicable if region of occurrence is known and when species-level results not essential	Applicable when species-level results not essential; potential to make results more species-specific by using traits to interpret likely threats and opportunities arising due to region's exposure to climate changes	Applicable when species-level results not essential; potential to make results more species-specific by using traits to interpret likely threats and opportunities arising due to region's exposure to climate changes and by considering impacts on drivers of species decline

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892	**RED LIST ASSESSMENTS AND CCVA**

893	The three-step assessment protocol outlined above parallels that recommended for assessing
894	species' extinction risks under climate change using the IUCN Red List criteria (IUCN SSC Standards
895	and Petitions Subcommittee, 2017, section 12.1). Red List assessments use information on threats
896	(including their spatial spread and projected severity), symptoms of endangerment (e.g. size and
897	trends of population and range area, fragmentation and fluctuations), and life history traits (e.g.
898	generation time, mating system, dispersal ability) to estimate or infer a number of variables such as
899	reduction in geographic range and population size, and thereby to determine species' extinction
900	risks. Identifying likely mechanisms of climate change impacts helps to define key variables needed
901	in Red List assessments. Each of the three CCVA stages for quantifying impacts (Step 3) can produce
902	results that are applicable to Red Listing. Table 8 links these stages to the Red List parameters they
903	can inform and the subsequent Red List criteria to which these apply. Expert or trait-based
904	assessment, for example, may reveal that a focal species has a very restricted distribution which is
905	subject to an immediate threat, thereby triggering a Red Listing of Vulnerable under criterion D2.
906	However, in order to project distribution and/or population declines and hence apply criteria A and
907	C1, correlative, mechanistic and/or combined approaches are required.

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910	*Table 8. Relationships between CCVA Assessment Stages and approaches, Red List parameters and*
911	*and Red List Assessment criteria (in parentheses)*

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Assessment stage and approach	Relevant Red List parameters
Stage 1: Expert and trait-based assessment	• Very restricted distribution and the plausibility and immediacy of threat (D2) • Number of locations (B, D2) • Severe fragmentation (B, C2) • Extreme fluctuations (B, C2) • Continuing decline (B, C2) • *Suspected* population reduction (A)
Stage 2: Correlative assessment and correlative-trait combinations	• Estimated continuing decline (C1) • *Inferred* or *projected* population reduction (A)
Stage 3: Mechanistic assessment and mechanistic-correlative-trait combinations	• Estimated continuing decline (C1) • *Projected* population reduction (A) • Probability of extinction (E)

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FUTURE DIRECTIONS

CCVA validation

Validation of CCVAs is an important process that identifies how well the different methods are performing. This is crucial both for understanding uncertainty in current assessments and for guiding model choice and development for future assessments. Comparisons of the results of different CCVAs have highlighted variable results when considering the same species (Lankford *et al.*, 2014; Wheatley *et al.*, 2017), so identifying which approaches are most effective is essential to aid conservation practitioners and policy makers when making decisions based on the CCVA outputs.

Most of the approaches applied to CCVA validation to date have been focussed on the performance of ecological niche models and similar correlative methods, testing model-based predictions across space and through time. The most commonly used approach involves repeatedly fitting models using randomly selected subsets of the available data from a single time period (e.g. 70% of the records), with performance of the model assessed on how well the remaining data are predicted by them (Araújo *et al.* 2005; Pearson *et al.*, 2007; Hole *et al.*, 2009; Araújo *et al.*, 2011; Garcia *et al.*, 2012). However, this can lead to an overestimation of predictive ability, because data in the test set are spatially autocorrelated with those used for calibration (Beale *et al.*, 2008). Where possible, it is preferable to predict a species' distribution in one geographic region based on a model fitted to records from a different region (Beerling *et al.*, 1995; Randin *et al.*, 2006), again comparing the predicted distribution with the actual distribution data for the non-modelled region to assess how well the model has performed. Alternatively, geographic partitioning of the study area can generate validation data that are more spatially independent than data resulting from random sub-setting (Morueta-Holme *et al.*, 2010; Wenger & Olden, 2012). In this case, the study area is divided into distinct geographic sections, such as spatially clustered tiles or longitudinal bands, and the model is fitted and evaluated with records from distinct sections.

Both of these approaches (random subsets and 'out of area') only consider model performance during the same timeframe, which may be of limited applicability for a model that is designed to assess temporal changes in response to climate change. One way to improve this is to use the model to predict distribution in another time period (either forward or backwards in time; Hill *et al.*, 1999; Araújo *et al.*, 2005; Morelli *et al.*, 2012; Bled *et al.*, 2013; Watling *et al.*, 2013; Huntley *et al.*, 2014). The model predictions can then be tested against actual records in the non-modelled time period or, most rigorously of all, tested against changes to the distribution or abundance either forwards or backwards through time (Green *et al.*, 2008; Gregory *et al.*, 2009; Illan *et al.*, 2014; Stephens *et al.* 2016). Such tests have demonstrated that correlative methods can have useful predictive power when modelling changes in distribution or abundance, and therefore may be informative when predicting species vulnerability under climate change.

Combined CCVAs incorporate different (depending on the specific method) types of information about the attributes of species, environments they occupy, and their empirical population and distribution trends, as well as ctorrelative model-based projections. There has been relatively little

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956 validation of trait-based CCVAs, although it is possible to do so by comparing results of the
957 assessment for a species against observed changes in that species' distribution or abundance under
958 climate change (where available). One recent study (Wheatley *et al*., 2017) using this approach
959 found that trait-only CCVAs did not predict changes in status through time successfully whereas
960 methods that included population and/or distribution trends (incorporating correlative projections)
961 as well as some trait information (e.g. habitat and dispersal constraints) could predict changes in
962 status. This validation was limited to one geographic region over a relatively short time period, so
963 further work is required to broaden the scope of CCVA validation and establish which methods work
964 best under different circumstances.

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966 **Improving biodiversity data**

967 The absence of readily available, research-quality data on species' distributions, physiological
968 tolerances, interspecific interactions and ecological traits limits the application of CCVA methods for
969 many species, especially those in non-charismatic groups and/or poorly-studied regions (Foden *et*
970 *al.*, 2013; Butt *et al.*, 2016; Supplementary Table 7). The poor coordination and disharmony of
971 existing biodiversity observations are additional challenges (Scholes *et al*., 2012; Joppa *et al*., 2016).
972 Increasing the quantity, quality and coordination of biodiversity data is therefore a priority to allow
973 application of CCVA methods to more species, validate CCVA outputs, enable more widespread use
974 of mechanistic models and perform the monitoring needed to integrate climate change adaptation
975 into conservation plans and actions. Furthermore, recognition of the value of trait variability in
976 addition to species means will improve predication accuracy (Cordlandwehr *et al*., 2013).
977 Encouraging signs are the increasing availability of digital locality data through portals such as the
978 Global Biodiversity Information Facility, published trait databases (e.g. Oliveira *et al*., 2017), and
979 citizen science schemes for sharing observational data (e.g. eBird, iNaturalist (Pearce-Higgins *et al*.,
980 2018). Progress towards imputing unknown trait data also helps fill data gaps (Penone *et al*., 2014;
981 Schrodt *et al*., 2015).

982 **Advancing CCVA methodology**

983 CCVA methodological development remains a fertile area of research. Combined or 'hybrid' methods
984 that draw on the strengths of the three approaches provide much promise. Inter-species
985 interactions are seldom explicitly considered in CCVAs, yet they can be important drivers of climate
986 change impacts on species (Ockendon *et al*., 2014); Schweiger *et al*. (2008, 2012) and Singer *et al.*,
987 (2018) provide notable exceptions and illustrate how such interactions may be included. Modelling
988 the dynamics of predator-prey, host-parasite and competitor dynamics (including those involving
989 invasive alien species) into the future represents a key gap and challenge. Better understanding of
990 how climate and non-climate pressures interact, and how to account for this interaction in CCVA
991 methods is another challenge (Segan *et al*., 2015). Greater attention to baselines, and accounting for
992 climate change that has already taken place (IPCC, 2013; van Wilgen *et al*., 2015; Huntley *et al*. 2018)
993 are needed to improve correlative approaches, especially for species with slow or lagged responses
994 to ongoing climate change. Trait-based models can be improved through better empirical data on

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995   thresholds associated with vulnerability for traits. As mentioned, incorporating the effects of human
996   responses to climate change into CCVAs is another area that requires additional development.

997   *Better consideration of climate extremes and variability*

998   Future climates will have more variability and more frequent extreme events, although to date these
999   remain poorly projected by earth system models. Nonetheless, together these will likely have
1000   greater effects on ecological systems than shifts in means alone (Thompson *et al.*, 2013). Extreme
1001   events are challenging to evaluate due to their rarity. Ameca y Juárez *et al.* (2013) analysed impacts
1002   of cyclones and droughts on terrestrial mammals, and Thompson *et al.* (2013) proposed a method
1003   for using downscaled climate projections that incorporate changes in climate variability. Despite the
1004   important roles that variability and extremes play in determining patterns of biological diversity, the
1005   ecology and conservation communities are just beginning to address the impacts of catastrophic
1006   events (Butt *et al.*, 2016; Palmer *et al.* 2017).

1007   **Incorporating molecular information**

1008   Molecular data can help in CCVA analyses by providing information on population processes such as
1009   modes of reproduction, past and current dispersal patterns, and changes in population size.
1010   Molecular analyses have traditionally involved microsatellite (=SSR) markers consisting of variation
1011   in the number of short tandem repeats ('microsatellites') at various locations in an organism's DNA,
1012   as well as sequence variation in mitochondrial (mt) and chloroplast (cp) DNA. However, in recent
1013   years there has been a rapid shift from scoring variation in a few (10-30) microsatellite markers to
1014   using thousands of SNP (single nucleotide polymorphism) markers across genomes, since new
1015   sequencing technologies mean that these can now be screened cheaply using non-invasive sampling
1016   (Allendorf, 2017). SNP markers provide a more detailed and accurate picture of population
1017   processes (Çilingir *et al.*, 2017; Younger *et al.*, 2017), including the way in which populations have
1018   expanded and shrunk historically, and their interactions with other populations. Molecular markers
1019   indicate whether ongoing exchange of genes across populations or species has occurred which may
1020   bolster the species' adaptive capacity (Garcia-Elfring *et al.*, 2017).

1021   As information on the genomics and transcriptomics of many groups of organisms increases,
1022   molecular SNP markers are increasingly being used to test for local adaptation across species ranges
1023   (Hoffmann *et al.*, 2015; Allendorf, 2017). Such tests have traditionally relied on controlled
1024   experiments in which populations from different environments are reared under common
1025   conditions and/or translocated between sites; these tests are difficult and time-consuming to
1026   undertake for long-lived species and may not deliver results in a sufficiently timely manner,
1027   particularly for already-threatened species. However, local adaptation to different climates can also
1028   be identified by testing whether genomic markers are correlated with environmental gradients (e.g.
1029   Steane *et al.*, 2014; Schweizer *et al.*, 2016; Harrisson *et al.*, 2017), which in turn can be used to
1030   predict whether gene pool mixing can bolster adaptive capacity (He *et al.*, 2016; Jordan *et al.*, 2017).
1031   Molecular data can also be combined with phenotypic information on species to determine whether
1032   translocations to boost natural populations are successful at increasing fitness (Christmas *et al.*,

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1033 2016) and to assess the effects of hybridization on species as climate shifts their distributions and
1034 increases the likelihood of hybridisation (Janes & Hamilton, 2017).

1035 **Incorporating adaptive genetic change and phenotypic plasticity**

1036 At this stage it is still unclear how quickly species can adapt genetically or plastically to counter the
1037 effects of climate change. While species can exhibit genetic adaptation over remarkably short time
1038 scales, CCVA-relevant information on the potential of species to undergo evolutionary adaptation to
1039 climate change is relatively scarce (Catullo *et al*., 2015; Nicotra *et al*., 2015; Beever *et al*., 2016). In
1040 models where evolutionary adaptation has been incorporated into CCVAs, the impact of
1041 evolutionary adaptation can be substantial at least in species with relatively short generation times
1042 (Bush *et al*., 2016). However evolutionary adaptation depends on the availability of adequate
1043 heritable variation on which selection can act, and relevant information on such heritable variation is
1044 currently only available for a few species. Plasticity can have a large impact on the adaptive potential
1045 of populations, particularly through phenological changes that adjust the timing of activity and
1046 reproduction of organisms (Merilä & Hendry, 2014). However, while many plastic changes in
1047 response to climate change are adaptive in populations, this is not always the case, particularly
1048 when the entire range of a species is considered (Duputié *et al*., 2015). Guidelines on the
1049 development and maintenance of adaptive capacity are currently being developed for incorporation
1050 into CCVAs (Beever *et al*., 2016).

1051 **Approaches to uncertainty**

1052 Since each component of data used in CCVA is associated with a degree of uncertainty, the overall
1053 CCVA has a level of uncertainty derived from all component datasets. Data omitted due, for
1054 example, to unavailability contributes further (Patt *et al*., 2005). High uncertainty over species-
1055 specific assessments is therefore to be expected, even where there is high confidence in the general
1056 direction of projected trends (Pearce-Higgins *et al*., 2017; Wheatley *et al*., 2017). Despite the large
1057 literature on this topic (Patt *et al*., 2005; Glick *et al*., 2011), more transparent, precise and consistent
1058 approaches are needed to estimate and/or communicate the nature of uncertainty. 'Maps of
1059 ignorance' (Rocchini *et al*., 2011) and 'Value-suppressing uncertainty palettes' (Correll *et al*., 2018),
1060 for example, are effective ways of conveying uncertainties associated with predictions of species'
1061 future ranges. Effective and targeted communication of CCVA results, drawing from lessons learnt
1062 from the public climate change debate (Moser, 2010; Pidgeon & Fischhoff, 2011), can increase the
1063 likelihood that findings will be used, including to inform adaptation strategies for focal species.

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1067 **CONCLUSION**

1068 Understanding species' vulnerability to climate change plays a vital role in developing effective
1069 biodiversity conservation plans. This has driven the emergence of an exciting new field and a rapidly
1070 growing literature. With a dizzying number of studies available and more published every day,
1071 practitioners can easily be overwhelmed. New and existing concepts and terms have been variously
1072 interpreted, creating challenges for those wishing to apply them. Nevertheless, the field is now
1073 mature enough to summarize best practices and recommend approaches to apply today. We borrow
1074 from the time-tested Driver-Pressure-State-Impact-Response (DPSIR) framework (Kristensen, 2004;
1075 Svarstad *et al*., 2008; Omann *et al*., 2009), and stress the importance of identifying and quantifying
1076 particular mechanisms that underlie climate change impacts on species of interest, since these
1077 directly inform appropriate conservation responses.

1078 Quantification of the vulnerability conferred to species through impact mechanisms is a central
1079 CCVA theme. We describe four commonly applied CCVA approaches, namely trait-based, correlative,
1080 mechanistic and combined approaches, highlight advantages and disadvantages of each, and
1081 providing examples of their use. Because mechanistic methods (and approaches that combine
1082 mechanistic with another method) can potentially quantify multiple mechanisms of climate impact
1083 as well as interactions between climate change and non-climate change related pressures, these
1084 approaches provide an obvious advantage. However, mechanistic methods are data and resource
1085 intensive. Practitioners typically face real-world limitation of resources (e.g. time, money, data,
1086 expertise), leaving as options only less intensive and less detailed approaches, which now
1087 nonetheless produce valuable outputs (Martin *et al*., 2012, 2017). Because poorly-known, small- and
1088 declined-range species are often of high priority for conservation and pose particular challenges for
1089 CCVA, we highlight possible approaches for their assessment. We also discuss the use of CCVA to
1090 inform Red List assessments of extinction risk.

1091 Any CCVA approach can deliver unreliable or misleading results when incorrect input data and
1092 parameters are applied. We therefore provide guidance on selecting and using CCVA input data for
1093 estimating species' sensitivity and adaptive capacity, as well as for measuring exposure to pressures
1094 driven by abiotic climate change-related pressures (i.e. climate change, elevated greenhouse gasses,
1095 physical environment changes), biotic pressures (e.g. biotic interactions, ecosystem changes), and
1096 human responses to climate change. A growing body of valuable open-access CCVA resources is
1097 available, and we provide links and references for locating a selection of these. We also outline ways
1098 to communicate CCVA results in a range of contexts to maximize influence on conservation planning
1099 and management decisions.

1100 Finally, we look to the future of CCVA and highlight some of the directions that we see as important
1101 avenues for further development and research. Most importantly, as observable climate change
1102 impacts on species become widespread, they provide opportunities to improve understanding of
1103 impact mechanisms and to test and validate CCVA assessments. Stepping up such validation and
1104 using results to improve CCVA of species is critical. We recognise the need for improving quantity,
1105 quality, and availability of biodiversity data, and advancing CCVA methodology, particularly through
1106 consideration of climate extremes and variability and of the effects of human responses to climate

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1107 change. Lastly, we discuss developments in molecular biology and their potential application for
1108 improving CCVA of species.

1109 As change to Earth's climates accelerates, managers and policy makers must become increasingly
1110 informed by CCVAs. The current strategic goals for biodiversity set by the Convention on Biological
1111 Diversity expire in 2020 and largely ignore climate change. To be effective, the post 2020 biodiversity
1112 agenda will need to be more explicit on protecting biodiversity under climate change, thus elevating
1113 the role of CCVA and requiring even more rigor in its application.

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1117 **FURTHER READING**

1118 **Resources for climate change adaptation and vulnerability assessment**
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1120 • IUCN Species Survival Commission: Guidelines for Assessing Species' Vulnerability to Climate
1121 Change (Foden & Young, 2016)
1122 • Responding to Climate Change: Guidance for Protected Area Managers and Planners. Developed
1123 by the IUCN World Commission on Protected Areas (Gross *et al.*, 2016).
1124 • Climate-Smart Conservation: Putting Adaptation Principles into Practice. Developed by the US
1125 National Wildlife Federation (Stein *et al.*, 2014).
1126 • Climate Change Vulnerability Assessment for Natural Resources Management: Toolbox of
1127 Methods with Case Studies. Developed by the US Fish and Wildlife Service (Johnson, 2014).
1128 • The Adaptation for Conservation Targets (ACT) Framework: A Tool for Incorporating Climate
1129 Change into Natural Resource Management (Cross *et al.*, 2012, 2013).
1130 • Scanning the Conservation Horizon: A Guide to Climate Change Vulnerability Assessment.
1131 Developed by a workgroup of US government, non-profit, and academic institutions (Glick *et al.*,
1132 2011).
1133 • Climate Change and Conservation: A Primer for Assessing Impacts and Advancing Ecosystem-
1134 based Adaptation in The Nature Conservancy (Groves *et al.*, 2010).
1135 • Voluntary guidance for states to incorporate climate change into state wildlife action plans and
1136 other management plans. Developed by the Association of Fish and Wildlife Agencies
1137 (Association of Fish and Wildlife Agencies, 2009).
1138 • Species' Distribution Modeling for Conservation Educators and Practitioners (Pearson, 2007).
1139 • Habitat Suitability and Distribution Models (Guisan *et al.*, 2017).
1140 • Online Open Course in Species Distribution Modeling (Huijbers *et al.*, 2016).
1141 • Biodiversity and Climate Change Virtual Laboratory (Hallgren *et al.*, 2016).
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1144   **FIGURES AND TABLES**

1145   [Figures 1-6 and Tables 1-8 are included in the body of the text as instructed]

1146

1147   **Sidebar title:**

1148   [Box 1 included in body of the text as instructed]

1149

1150   **ACKNOWLEDGMENTS**

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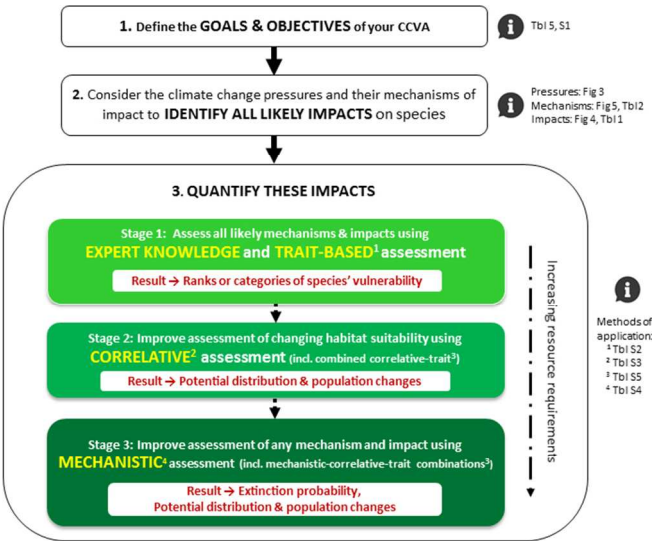2119   Thomas C.D., Hill J.K., Anderson B.J., Bailey S., Beale C.M., Bradbury R.B., Bulman C.R., Crick H.Q.P.,
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STEPS FOR CARRYING OUT
CLIMATE CHANGE VULNERABILITY ASSESSMENT OF SPECIES

1. Define the **GOALS & OBJECTIVES** of your CCVA — Tbl 5, S1

2. Consider the climate change pressures and their mechanisms of impact to **IDENTIFY ALL LIKELY IMPACTS** on species — Pressures: Fig 3 / Mechanisms: Fig 5, Tbl2 / Impacts: Fig 4, Tbl 1

3. QUANTIFY THESE IMPACTS

Stage 1: Assess all likely mechanisms & impacts using **EXPERT KNOWLEDGE** and **TRAIT-BASED**[1] assessment
Result → Ranks or categories of species' vulnerability

Stage 2: Improve assessment of changing habitat suitability using **CORRELATIVE**[2] assessment (incl. combined correlative-trait[3])
Result → Potential distribution & population changes

Stage 3: Improve assessment of any mechanism and impact using **MECHANISTIC**[4] assessment (incl. mechanistic-correlative-trait combinations[3])
Result → Extinction probability, Potential distribution & population changes

Increasing resource requirements

Methods of application:
[1] Tbl S2
[2] Tbl S3
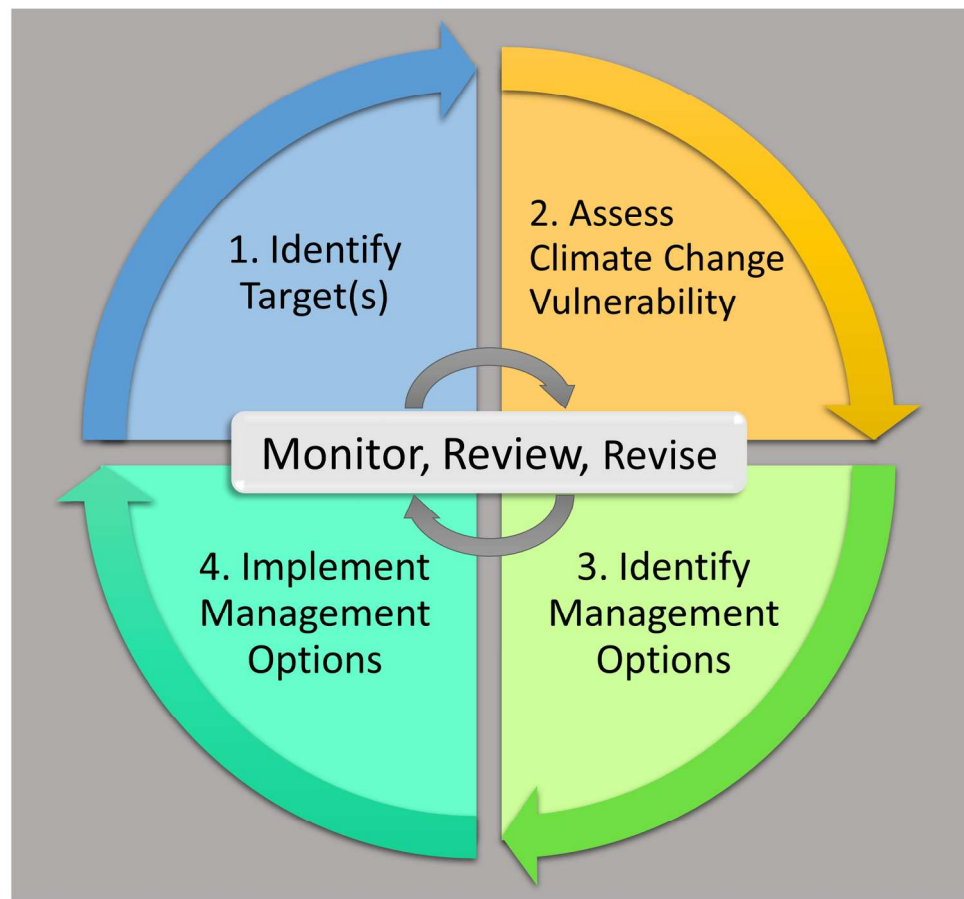[3] Tbl S5
[4] Tbl S4

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Figure 1: Steps for developing climate change adaptation strategies (Adapted from Glick et al. (2011))
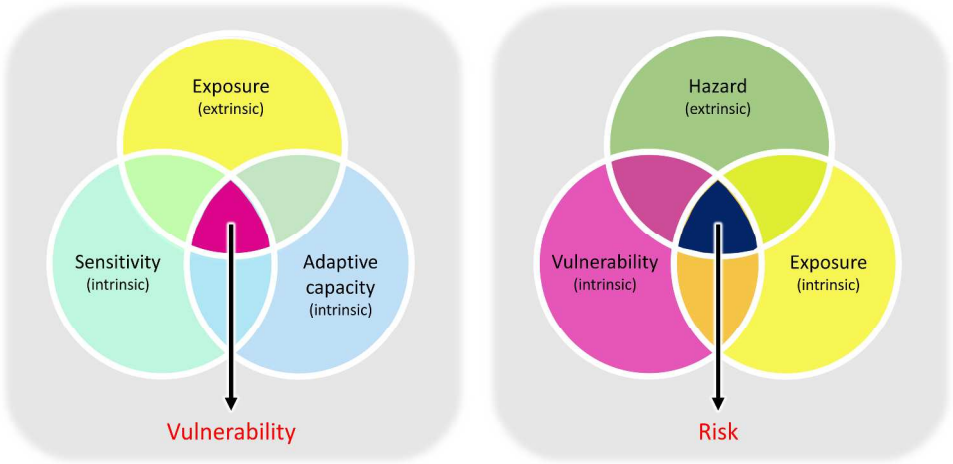
174x162mm (300 x 300 DPI)

Figure 2a. According to the IPCC Fourth Assessment (2007) and common usage in the field of CCVA of species, vulnerability to climate change results from the interaction of exposure and sensitivity with adaptive capacity (adapted from IPCC, 2007).

Figure 2b. According to the IPCC Fifth Assessment (2014), risk of climate-related impacts results from the interaction of climate-related hazards with the vulnerability and exposure of human and natural systems (adapted from IPCC (2014)).
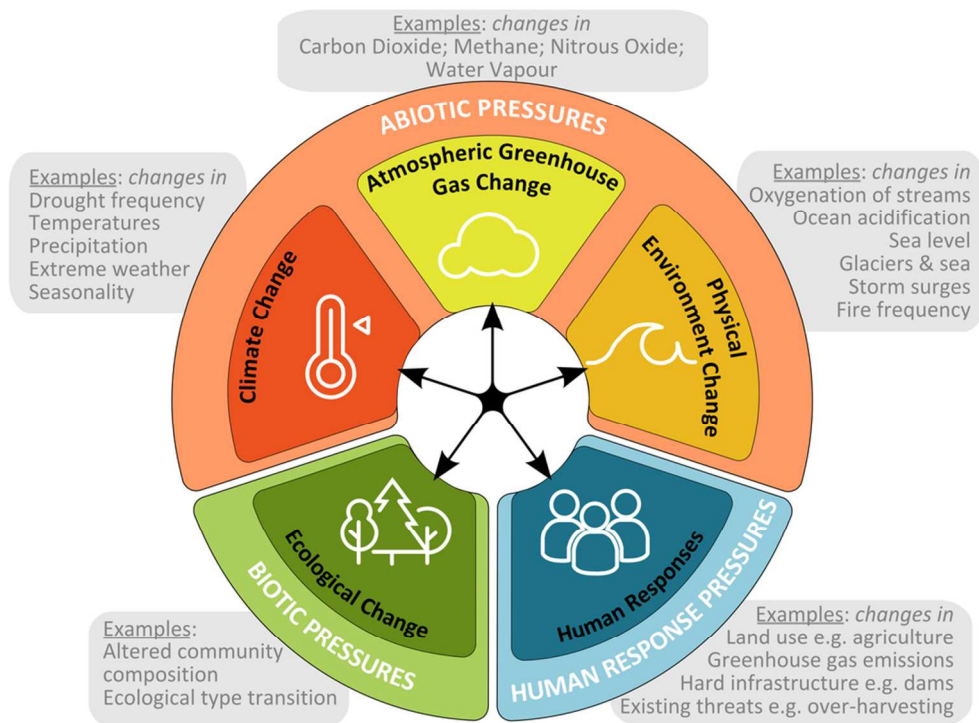
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Figure 3. Climate change related pressures on species, showing those originating from abiotic, biotic and human response causes.
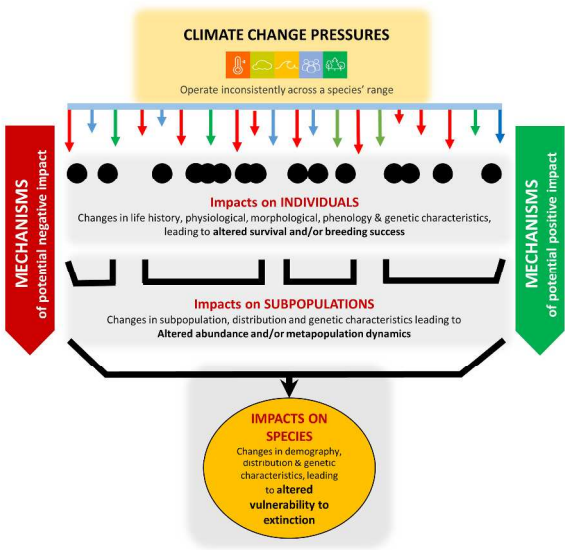
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Figure 4. Potential climate change impacts on species include the species-level population and range changes that underpin extinction risk. These changes are driven by changes at individual and subpopulation levels.
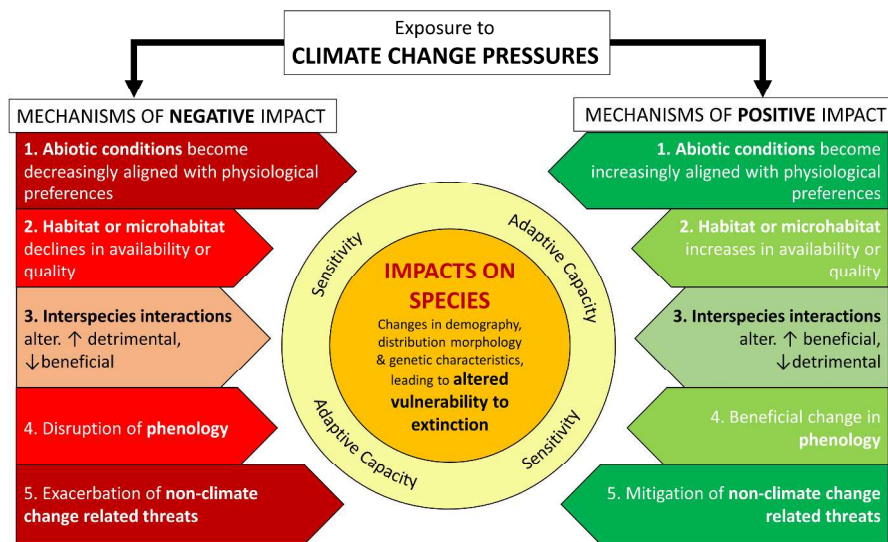
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Figure 5. Mechanisms describe the pathways through which climate change pressures may exert impacts on species. These impacts may have positive and/or negative impacts on the species and are mitigated or exacerbated by species' individual sensitivities and adaptive capacities.

338x190mm (300 x 300 DPI)

STEPS FOR CARRYING OUT
CLIMATE CHANGE VULNERABILITY ASSESSMENT OF SPECIES

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Result → Extinction probability,
Potential distribution & population changes

Increasing resource requirements

Methods of application:
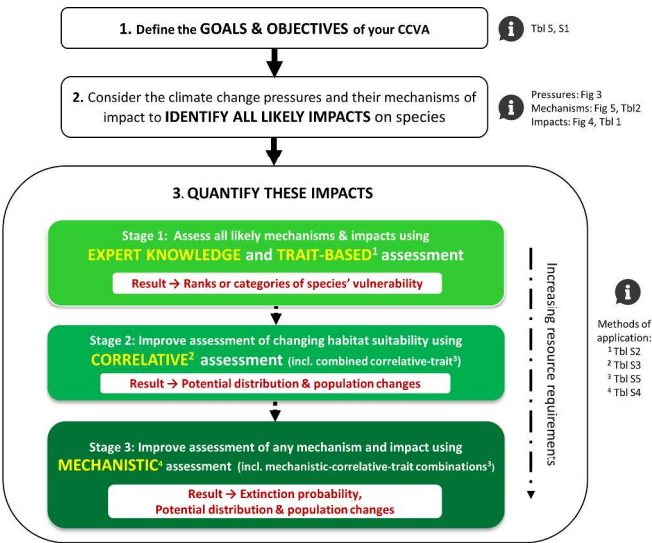[1] Tbl S2
[2] Tbl S3
[3] Tbl S5
[4] Tbl S4

Figure 6. The approaches used to carry out each of the three assessment types and the metrics or types of information of climate change vulnerability that they may produce.

190x338mm (300 x 300 DPI)