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## Climate change vulnerability assessment of species

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# CLIMATE CHANGE VULNERABILITY ASSESSMENT OF SPECIES

Article Type: Overview

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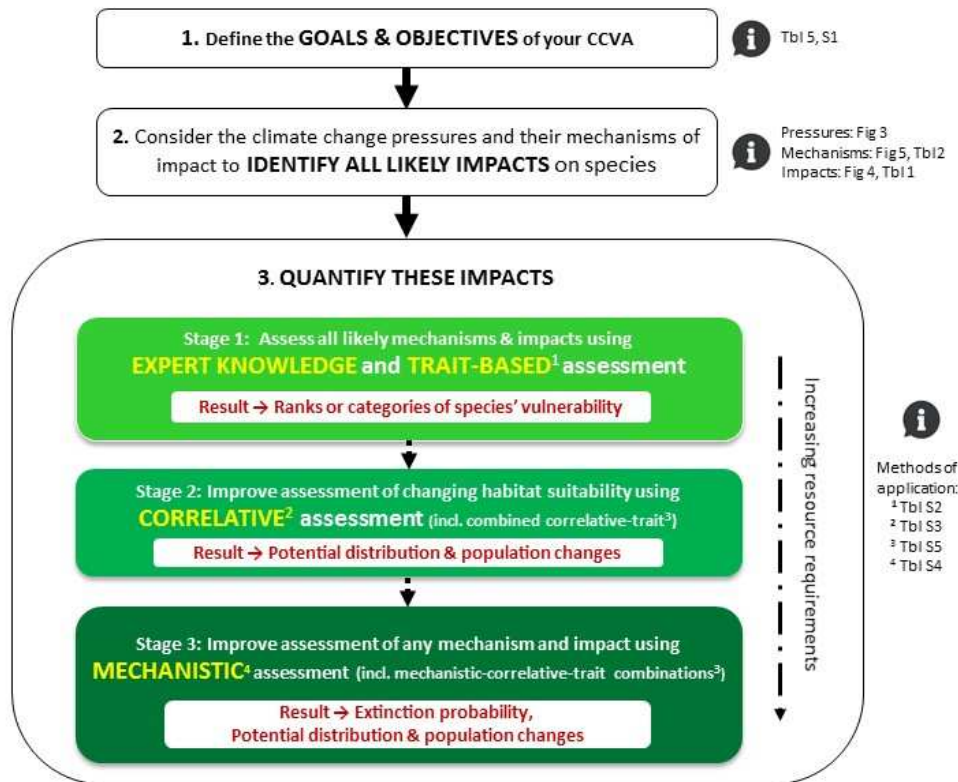
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## ABSTRACT

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**

31 **STEPS FOR CARRYING OUT**  
 32 **CLIMATE CHANGE VULNERABILITY ASSESSMENT OF SPECIES**



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.

36

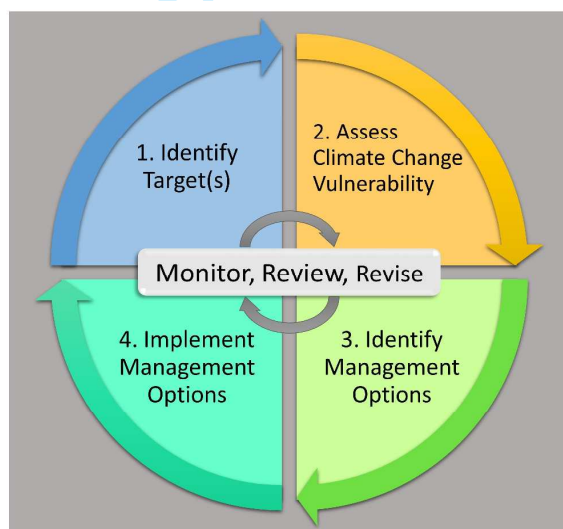
37 **INTRODUCTION**

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

47 The Bramble Cay Melomys joins a rapidly growing number of species for which the impacts of  
48 anthropogenic climate change have been documented. These species span: different biological  
49 kingdoms, including plants and animals; most latitudes, including polar, temperate, subtropical and  
50 tropical; many ecosystems, including those of the marine, freshwater and terrestrial realms; all the  
51 principal terrestrial biomes, from tundra to equatorial rainforest; and most habitat types, including  
52 coral reefs, forests, deserts, grasslands and wetlands (e.g. Gardner *et al.*, 2015; Hughes *et al.*, 2003;  
53 Pounds *et al.*, 2006; Chen *et al.*, 2009; Doney *et al.*, 2011; Whinam *et al.*, 2014; Mason *et al.*, 2015a;  
54 Ramula *et al.*, 2015; Scheffers *et al.*, 2016). Within species, impacts have been shown at levels from  
55 genes and individuals to populations, and changes in composition of communities and in inter-  
56 specific interactions are also prevalent (e.g. Gardner *et al.*, 2015; Chen *et al.*, 2011; Ramula *et al.*,  
57 2015; Scheffers *et al.*, 2016). These impacts have occurred at global mean temperature increases of  
58 less than 1°C, yet without major reductions in emissions of carbon dioxide and other greenhouse  
59 gases, a rise of 2°C or more is increasingly probable. As a result, many more impacts including  
60 species declines and extinctions are likely, with the potential to undermine ecosystem health and  
61 function (Martin & Watson, 2016; Pecl *et al.*, 2017).

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

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))*

## 95 **THE EMERGENCE OF CLIMATE CHANGE VULNERABILITY ASSESSMENT**

96 Although the influence of the atmospheric concentration of carbon dioxide on global climate had  
 97 been identified already in the late 19<sup>th</sup> 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

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2  
3 100 landmarks as the SCOPE 29 volume (Bolin *et al.*, 1986) that addressed the potential impacts upon  
4 101 ecosystems both of projected climate changes and of the direct effects of increasing carbon dioxide  
5 102 concentration. In 1987 the International Council of Scientific Unions established the International  
6 103 Geosphere–Biosphere Programme that stimulated international research organised around six core  
7 104 projects, including ‘Global Change and Terrestrial Ecosystems’, and that led to numerous influential  
8 105 publications (e.g. Walker & Steffen, 1996). The rapid growth in international concern also led to the  
9 106 establishment in 1988 of the Intergovernmental Panel on Climate Change (IPCC) that produced its  
10 107 first report in 1990 in which it discussed, albeit briefly, the potential impacts upon biodiversity and  
11 108 identified the potentially most vulnerable ecosystems (Street *et al.*, 1990). The implications for  
12 109 conventional approaches to biodiversity conservation began to be discussed around the same time  
13 110 (e.g. Hunter, Jacobson, & Webb, 1988; Huntley & Webb III, 1988) and the lessons that could be  
14 111 learned from studies of Quaternary palaeoecology also began to be discussed (e.g. Huntley & Webb  
15 112 III, 1988; Huntley, 1990, 1991). Subsequently the volume edited by Peters & Lovejoy (1992)  
16 113 represented a key milestone on the road towards formalised assessments of species’ vulnerabilities  
17 114 to climate changes.  
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22 116 Climate change vulnerability assessment as a field emerged in the 1990s, drawing on several  
23 117 disparate disciplinary traditions, including natural hazard and disaster planning, climate change  
24 118 effects research, and endangered species conservation. The concepts behind vulnerability were  
25 119 originally and most fully developed in relation to risks from natural hazards to people and  
26 120 communities. Indeed, the field of climate adaptation has been heavily influenced by the work of  
27 121 such natural hazards researchers as Gilbert F. White and colleagues, who emphasized the  
28 122 importance of social and technological ‘adjustments’ to these hazards (Burton *et al.*, 1993). Building  
29 123 on such disaster-related usage, early applications of vulnerability assessment in a climate change  
30 124 context primarily focused on susceptibility of people, infrastructure and economies to harm (Dow,  
31 125 1992; IPCC, 1996). Adger (2006) offered perhaps the most influential distillation of climate change  
32 126 vulnerability in a socioecological context, noting that ‘the key parameters of vulnerability are the  
33 127 stress to which a system is exposed, its sensitivity, and its adaptive capacity.’  
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38 129 Biogeographers, ecologists and conservation biologists began to explore the potential impacts of  
39 130 climate change on species and ecosystems during the early and mid-1990s (e.g. Lindenmayer *et al.*,  
40 131 1991; Huntley *et al.*, 1995; Sykes & Prentice, 1995; Sykes *et al.*, 1996). Around the same time  
41 132 observed effects of climate change on species’ distributions began to be documented (e.g. Grabherr  
42 133 *et al.*, 1994; Parmesan, 1996; Parmesan *et al.*, 1999) and the interacting effects upon species of  
43 134 climate change and habitat availability were discussed (e.g. Hill *et al.*, 1999). By the early 2000s, a  
44 135 range of effects of climate change on species was being widely documented (e.g. Hughes, 2000;  
45 136 Parmesan & Yohe, 2003), leading to more explicit interest in determining ‘which species, habitats  
46 137 and regions are most at risk from climate change’ (Pearson & Dawson, 2003), and the realisation  
47 138 that substantial numbers of species could be at risk of extinction (Thomas *et al.*, 2004). This in turn  
48 139 led to the application and modification of existing vulnerability frameworks (e.g. Schroter *et al.*,  
49 140 2005; Adger, 2006) for assessing natural systems, including plant and animal species (Williams *et al.*,  
50 141 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)**

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

climate change, to moderate potential damage, to take advantage of opportunities, or to respond to the consequences (IPCC, 2007, 2014)	<b>Exposure.</b> The <i>presence</i> 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) ( <i>Not defined in IPCC, 2007</i> )
<b>External Contributing Factors</b>	
<b>Exposure.</b> Exposure describes the nature, magnitude and rate of climatic and associated environmental changes experienced by a species (Dawson <i>et al.</i> , 2011; Foden <i>et al.</i> , 2013; Stein <i>et al.</i> , 2014) ( <i>Not defined in IPCC, 2007</i> )	<b>Hazard.</b> 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 <i>hazard</i> usually refers to climate-related physical events or trends or their physical impacts (IPCC 2014) ) ( <i>Not defined in IPCC, 2007</i> ).

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).

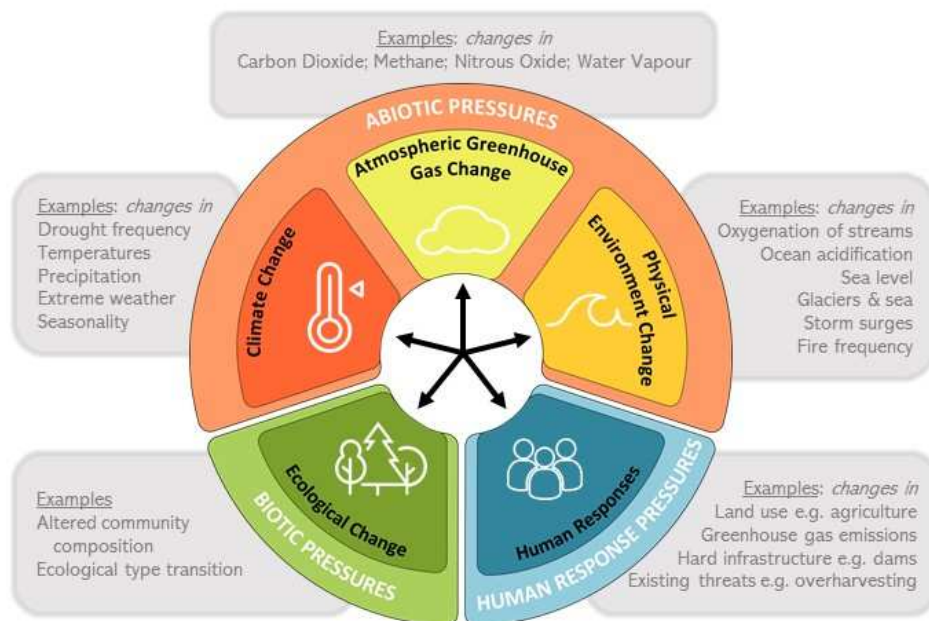
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169 *Drivers* are the highest order phenomena governing change; they typically encompass societal  
 170 demands or needs (e.g. economic, social, and political) and natural factors that are independent of  
 171 anthropogenic causes (e.g. earthquakes, 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

1  
2  
3 179 that includes three broad categories (Figure 3). *Abiotic pressures* include: climate changes driven by  
4 180 changes in atmospheric concentrations of greenhouse gases (e.g. increased temperatures, altered  
5 181 drought frequency); resulting effects on the physical environment (e.g. sea level rise, melting ice,  
6 182 increased severity of storm surges); and, direct effects of the changes in greenhouse gas  
7 183 concentrations (e.g. ocean acidification as a result of the increased atmospheric concentration of  
8 184 carbon dioxide). *Biotic pressures* result from changes in ecological processes (Ockendon *et al.*, 2014)  
9 185 and include those mediated through changes in habitat availability or community composition (e.g.  
10 186 increased competition from alien species), as well as direct effects of the changes in greenhouse gas  
11 187 concentrations (e.g. differential effects of elevated carbon dioxide levels on productivity of plants  
12 188 using alternative photosynthetic pathways). Finally, various societal actions resulting from climate  
13 189 change, including both from climate change mitigation (e.g. expansion of biofuel production,  
14 190 renewable energy technologies) and adaptation (e.g. changing land use, construction of dams and  
15 191 sea walls, water abstraction) may exert *human response pressures* on species that, although poorly  
16 192 recognised in vulnerability assessments, potentially have large impacts upon biodiversity (Turner *et al.*,  
17 193 2010; Watson & Segan, 2013; Maxwell *et al.*, 2015). This category also includes climate change  
18 194 driven exacerbation of historical human pressures such as harvesting and persecution. We note that  
19 195 pressures and drivers may be variously interpreted in ecological contexts, and that several authors  
20 196 have classified pressures as 'direct' (i.e. abiotic) and 'indirect' (i.e. biotic, and in some cases including  
21 197 human-mediated responses)(e.g. Chapman *et al.*, 2014; Ockendon *et al.*, 2014; Segan *et al.*, 2015).  
22 198 However, strong interactions and feedbacks between almost all contributing pressures (Figure 3)  
23 199 suggest that it is more realistic to consider biological responses as emerging from a complex network  
24 200 of interacting physical, biological and human processes.  
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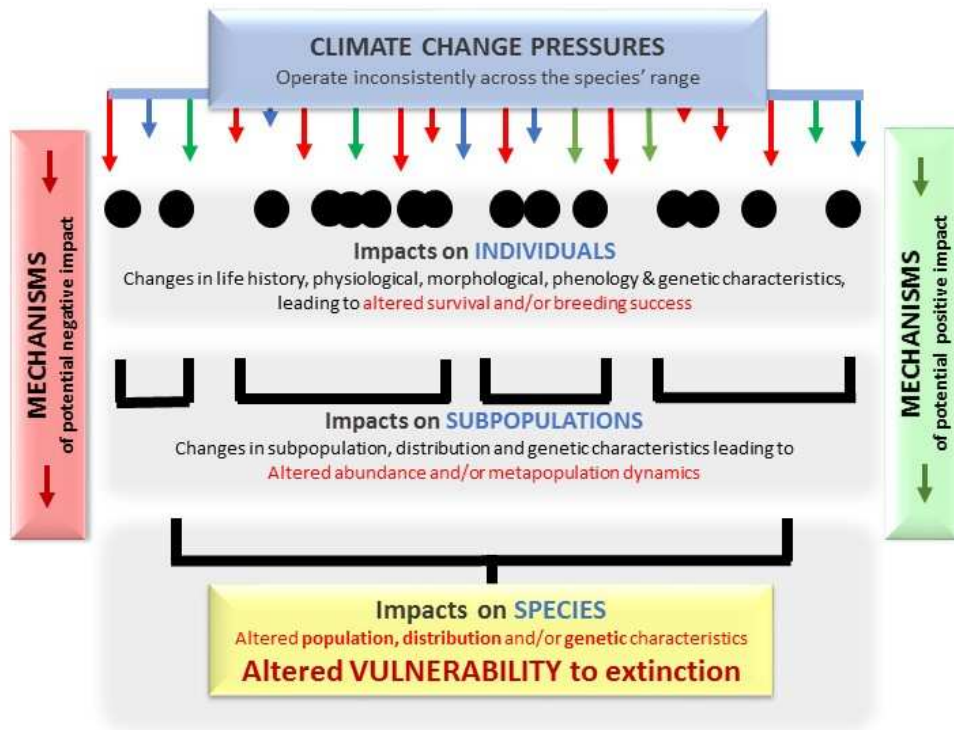
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1  
2  
3 203 *Figure 3. Climate change related pressures on species, showing those originating from abiotic, biotic*  
4 204 *and human response causes.*

5  
6 205

7 206 **Potential impacts and their mechanisms**

8  
9 207 Pressures exert influence on the *state* of systems (Oesterwind *et al.*, 2016) and may thereby lead to  
10 208 *impacts* on them (Svarstad *et al.*, 2008). The extent of impacts on species resulting from climate  
11 209 change associated pressures depends upon the intrinsic and external factors contributing to the  
12 210 species' vulnerability and may be positive, negative or a combination of both. In the context of CCVA  
13 211 of species, the focus is species' vulnerability to climate change-driven extinction, and the impacts are  
14 212 factors that influence this. Key parameters used by the IUCN Red List (IUCN, 2017) to assess a  
15 213 species' extinction risk are characteristics of, and changes in, its population size and distribution  
16 214 extent. While these parameters are appropriate at the species level, we note that they result from  
17 215 impacts on individuals that differ from one another both genetically and phenotypically with respect  
18 216 to their morphological, physiological, behavioural and life-history attributes (Figure 4 and Table 1).  
19 217 Individual-level impacts influence subpopulation characteristics, including local abundance and  
20 218 metapopulation dynamics, that in turn determine species-level parameters, including extinction risk  
21 219 (Griffiths *et al.*, 2010). It is important to realise that climate change will often have contrasting  
22 220 impacts on different organisms and local- or subpopulations of a species in different parts of their  
23 221 overall distribution. Thus, impacts are likely to be positive towards the 'leading edge' of a species'  
24 222 distribution, but negative towards the 'trailing edge', where leading and trailing edge are defined by  
25 223 the geographical gradient and direction of change of a climatic variable. The net results of these  
26 224 individual subpopulation-level impacts are changes in the species' overall population and  
27 225 distribution.



226

227 Figure 4. Potential climate change impacts on species include the species-level population and range  
 228 changes that underpin extinction risk. These changes are driven by changes at individual and  
 229 subpopulation levels.

230

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

Impacts	Illustrative examples
<b>SPECIES LEVEL</b>	
<b>1. Population characteristics</b> 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 <i>et al.</i> , 2016
<b>2. Range characteristics</b> 2.1. Changes in range size	Hickling <i>et al.</i> , 2006; Tingley <i>et al.</i> , 2009; Chen <i>et al.</i> , 2011;

2.2. Changes in range location 2.3. Level of fragmentation	Poloczanska <i>et al.</i> , 2013; Mason <i>et al.</i> , 2015
<b>3. Genetic characteristics</b> 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 <i>et al.</i> , 2014
<b>SUBPOPULATION LEVEL</b>	
<b>4. Subpopulation characteristics</b> 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 <i>et al.</i> , 2006; Martay <i>et al.</i> , 2017
<b>5. Range characteristics</b> 5.1. Changes in range sizes of subpopulations 5.2. Changes in range locations of subpopulations	Bennie <i>et al.</i> , 2013
<b>6. Genetic characteristics</b> 6.1. Changes in genetic diversity 6.2. Changes in allele frequencies 6.3. Changes in rates of gene flow between subpopulations	Kutschera <i>et al.</i> , 2016; Vincenzi <i>et al.</i> , 2017
<b>INDIVIDUAL LEVEL</b>	
<b>7. Life-history characteristics</b> 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 <i>et al.</i> , 1998; Barbraud & Weimerskirch, 2001; Aars & Ims, 2002; Ludwig <i>et al.</i> , 2006; Foley <i>et al.</i> , 2008; Robinson <i>et al.</i> , 2009; Martin & Maron, 2012
<b>8. Morphological characteristics</b> 8.1. Changes in body size 8.2. Changes in body shape	Rode <i>et al.</i> , 2010; Cheung <i>et al.</i> , 2012; Baudron <i>et al.</i> , 2014; Caruso <i>et al.</i> , 2014
<b>9. Physiological characteristics</b> 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 <i>et al.</i> , 2015
<b>10. Phenological characteristics</b> 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 <i>et al.</i> , 2010; Thackeray <i>et al.</i> , 2010; Todd <i>et al.</i> , 2010; Møller <i>et al.</i> , 2011; Lane <i>et al.</i> , 2012; R. Kearney, 2013

(e.g. a shift from diurnal to crepuscular or nocturnal activity)	
<b>11. Genetic characteristics</b>	Bradshaw & Holzapfel, 2001; Hill & Henry, 2011; Geerts <i>et al.</i> , 2015; Pacifici <i>et al.</i> , 2015; de Pous <i>et al.</i> , 2016
11.1. Changes in gene expression (e.g. due to epigenetic processes)	
11.2. Heterozygosity	

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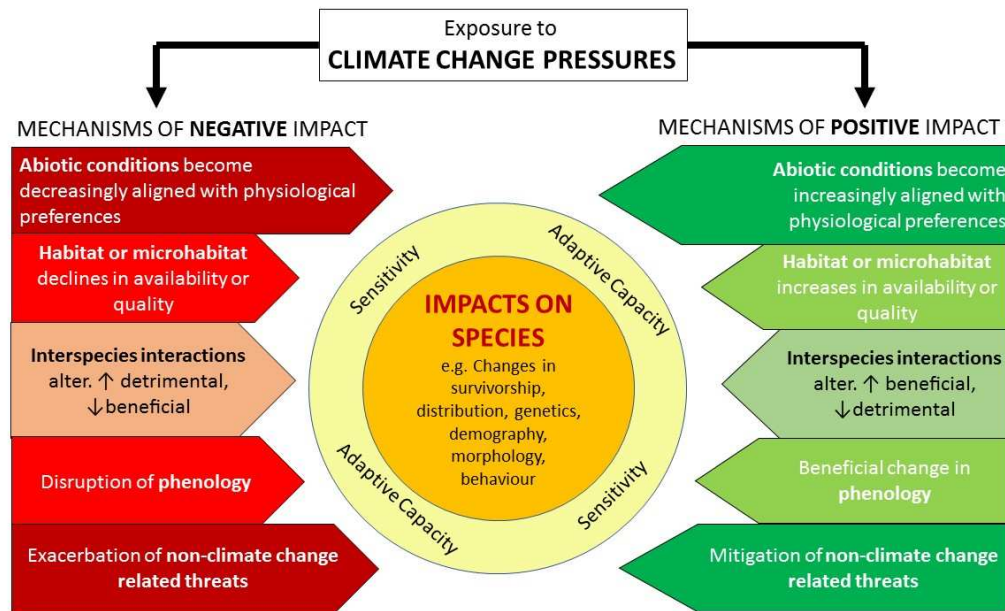
Understanding the *mechanisms* of potential climate change impacts on species, that is, the chain of events between the exertion of the pressure and the potential impacts at species level, is particularly valuable. Firstly, the degree of confidence associated with a projected climate change impact is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

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

POTENTIAL MECHANISMS OF IMPACTS ON SPECIES	Documented examples (+ve) or (-ve)
1. Organisms' <b>physiological preferences</b> or limits become decreasingly or increasingly aligned with changing <b>environmental conditions</b> .	Kullman, 2007; Oswald <i>et al.</i> , 2008; Pérez-Ramos <i>et al.</i> , 2010; Sinervo <i>et al.</i> , 2010; Beever <i>et al.</i> , 2011; Cahill <i>et al.</i> , 2013
2. Organisms' <b>habitat and microhabitats</b> 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 <i>et al.</i> , 2010; Rode <i>et al.</i> , 2010; Bond & Midgley, 2012; Martin & Maron, 2012
3. Organisms experience changes in <b>interspecific interactions</b> . This includes with <b>beneficial species</b> (e.g. prey, mutualists, hosts, pollinators, dispersers), <b>detrimental species</b> (e.g. competitors, predators, parasites, pathogens) and those that are currently <b>neutral</b> but may become beneficial or	Biesmeijer <i>et al.</i> , 2006; Schweiger <i>et al.</i> , 2008; Durance & Ormerod, 2010; Pearce-Higgins <i>et al.</i> , 2010

detrimental in the future.	
4. Organisms experience change in <b>phenology</b> such that the timing of beneficial events or interactions are disrupted or enhanced.	Visser <i>et al.</i> , 2006; Fryxell & Sinclair, 1988; Ludwig <i>et al.</i> , 2006; Altwegg <i>et al.</i> , 2012
5. Organisms experience changes in interactions with <b>non-climate change-driven threats</b> such that they are exacerbated (e.g. overharvesting, invasive species, land use changes)	Frederiksen <i>et al.</i> , 2004; Walther <i>et al.</i> , 2009; Schweiger <i>et al.</i> , 2010; Van Zuiden & Sharma, 2016; Kovach <i>et al.</i> , 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**

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

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

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

<b>Sensitivity Attributes</b>	
<b>A. Specialised habitat and/or microhabitat requirements.</b>	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>B. Environmental tolerances or thresholds (at any life stage) that are likely to be exceeded due to climate change.</b>	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 <i>et al.</i> , 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 <i>et al.</i> , 2007), high temperature-tolerant birds (Cunningham <i>et al.</i> , 2013)).
<b>C. Dependence on environmental triggers that are likely to be disrupted by climate change.</b>	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 <i>et al.</i> , 2016) (e.g. mismatches between advancing spring food availability peaks and hatching dates (Both <i>et al.</i> , 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 <i>et al.</i> , 2010).

**D. 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).

**E. 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.

**F. 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.

**G. 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.

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## 284 **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

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).  
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 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.  
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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)).*

<b>ADAPTIVE CAPACITY ATTRIBUTES</b>	
<b>A. Phenotypic plasticity.</b>	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 <i>et al.</i> , 2008) and are likely to remain important in the future for some common insectivorous passerines (Phillimore <i>et al.</i> , 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>B. Dispersal ability.</b>	Estrada <i>et al.</i> (2016) outline a framework highlighting four key factors that influence species' range-shifts, namely: (i) <b>Emigration.</b> 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 <i>et al.</i> , 2013). (ii) <b>Dispersal (movement ability):</b> <b>Intrinsic dispersal ability:</b> 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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3 accidental dispersal by mechanisms to which the species shows no particular adaptations were  
4 more important than dispersal adaptations and typical dispersal distances in achieving rapid and  
5 large range shifts (e.g. Wilkinson, 1997; Wilkinson *et al.*, 2017).

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

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

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

31  
32 **C. Evolvability.** Species' potential for rapid genetic change will determine whether evolutionary  
33 adaptation can result at a rate sufficient to keep up with climate change-driven changes to their  
34 environments. Species with low genetic diversity, often indicated by recent bottlenecks in population  
35 numbers, generally exhibit lower ranges of both phenotypic and genotypic variation. As a result, such  
36 species tend to have fewer novel characteristics that could facilitate adaptation to the new climate  
37 conditions.

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

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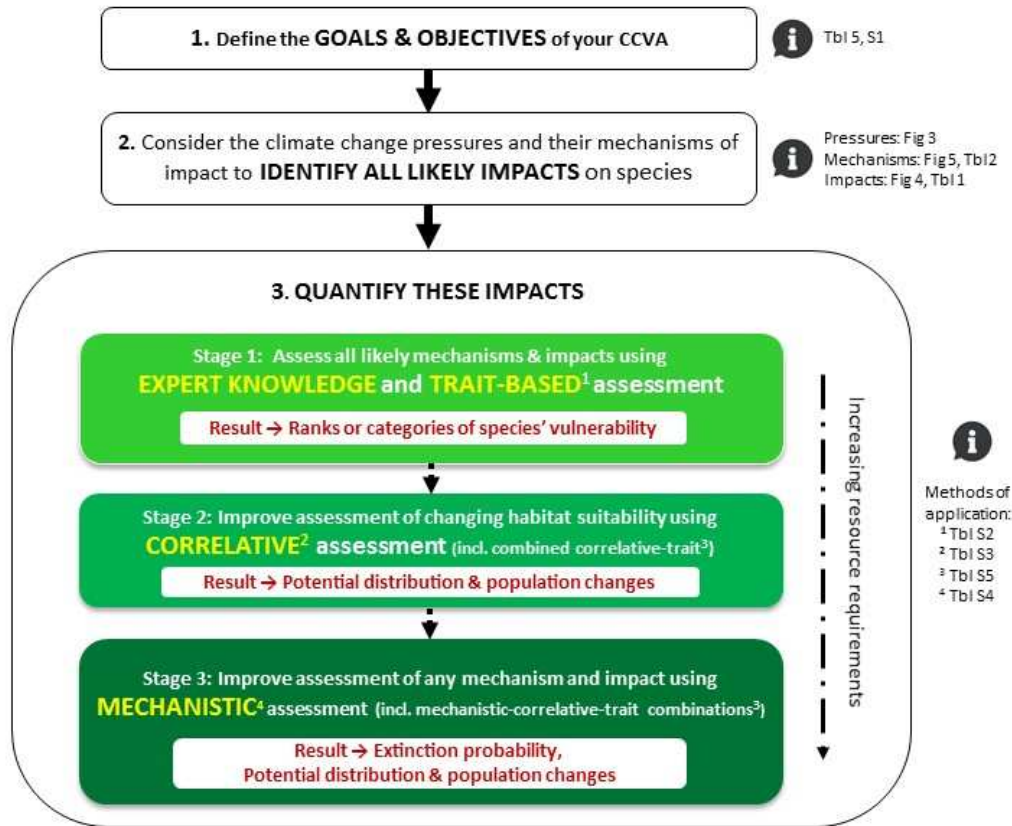
324 **CARRYING OUT CCVA OF SPECIES**

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

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**STEPS FOR CARRYING OUT  
CLIMATE CHANGE VULNERABILITY ASSESSMENT OF SPECIES**



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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.*

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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

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 <b>objective</b> category:						
	Which?	How much?	Why?	Where?	When?	What's missing?
Select a <b>taxonomic</b> focus (for example):						
	Subpopulation		Species	Higher taxonomic group	Multiple higher taxonomic groups	
Select a <b>spatial</b> 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 <b>time frame</b> (for example):						
	Present	5 years		20 years	50 years	100 years

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

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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.

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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.

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It is also valuable to explore whether CCVAs have already 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.

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**Step 3: Quantify the impacts**

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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

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3 406 correspond approximately with predominant CCVA approaches, namely *trait-based*, *correlative* and  
4 407 *mechanistic approaches*, while the *combined approach* is applicable to stages two and three. We  
5 408 outline each approach, discussing its strengths and limitations, methods of application, examples of  
6 409 use and the vulnerability metrics it delivers. More detailed discussions can be found in Pacifici *et al.*  
7 410 (2015).  
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9 412 In all cases, we recommend beginning with an expert-based assessment. This involves examining the  
10 413 range of likely impact mechanisms in relatively non-technical and non-statistically intensive ways,  
11 414 with the aim of categorising and potentially prioritising mechanisms according to their likely impacts  
12 415 on focal species. At the most basic level, this involves considering species' exposure to climate  
13 416 change pressures and, using available knowledge of the species' sensitivity and adaptive capacity to  
14 417 estimate the likely relative or absolute magnitude of the impacts on the species. Red List  
15 418 assessments may provide valuable information for such assessments because they help to identify  
16 419 species with demographic and/or behavioural characteristics that increase their sensitivity; they also  
17 420 identify other pressures faced by species that may be exacerbated by climate change.  
18 421 Notwithstanding their limitations, expert-based assessments provide a valuable foundation for  
19 422 identifying factors and mechanisms to focus on in subsequent stages.  
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#### 25 424 *Trait-based approach*

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27 425 This approach draws on the growing knowledge-base on associations between biological traits and  
28 426 climate change impacts (e.g. Cardillo *et al.*, 2008; Murray *et al.*, 2009; Thaxter *et al.*, 2010; Angert *et*  
29 427 *al.*, 2011; Chessman, 2013; Newbold *et al.*, 2013; Pearson *et al.*, 2014; Estrada *et al.*, 2015), and  
30 428 makes use of a range of biological and life history information to score or rank species' probable  
31 429 sensitivity and adaptive capacity to climate change. These are often combined with assessments of  
32 430 exposure (e.g. Williams *et al.*, 2008; Young *et al.*, 2012; Foden *et al.*, 2013b; Smith *et al.*, 2016).  
33 431 While in the strictest sense, 'traits' refer to the characteristics of an individual (Violle *et al.*, 2007), in  
34 432 the context of CCVA of species the term is generally used more loosely to refer to a broad range of  
35 433 species-level characteristics, examples of which are shown in Table 6 . Data relating to these traits  
36 434 may be qualitative, categorical or quantitative; categories must be ranked according to risk, whilst  
37 435 where trait data are quantitative, thresholds must be defined to determine risk categories. Trait-  
38 436 level scores or ranks are then combined qualitatively or semi-quantitatively to assign species into  
39 437 categories of vulnerability. We categorise methods for applying the trait-based approach according  
40 438 to the ways in which their scores are developed (i.e. Qualitative vs. Semi-Qualitative) and describe  
41 439 available tools, data requirements and examples (Supplementary Table 3). Trait-based approaches  
42 440 may include the outputs of correlative and mechanistic approaches (e.g. Küster *et al.*, 2011; Young *et*  
43 441 *al.*, 2012; Pompe *et al.*, 2014) or be included in other approaches (e.g. Garcia *et al.*, 2014a); we  
44 442 discuss these further under the 'Combined approach'.  
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50 444 Because the trait-based approach requires ecological knowledge without strong modelling or  
51 445 statistical expertise, and because it facilitates assessment of large numbers of species relatively  
52 446 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.

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

	Graham <i>et al.</i> (2011)	Gardali <i>et al.</i> (2012)	Garnett <i>et al.</i> (2013)	Foden <i>et al.</i> (2013)	Young <i>et al.</i> (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		

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#### 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

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3 469 species' realised niche (Hutchinson, 1957) during the period to which the distribution and climate  
4 470 data relate and can be used to infer its climate requirements or ecological tolerances. Correlative  
5 471 assessments can be used to identify those geographical areas where climate is likely to be suitable  
6 472 for the species under any projection of potential future climate (Pearson & Dawson, 2003; Beale *et al.*,  
7 473 *et al.*, 2008), and hence to estimate its potential distribution under those climate conditions. A species'  
8 474 climate change vulnerability is inferred from differences between its recent distribution and its  
9 475 predicted potential future distribution in terms of extent, location and sometimes degree of  
10 476 fragmentation (e.g. Garcia *et al.*, 2014a), and also their degree of overlap (Huntley *et al.*, 2007).  
11 477 Correlative approaches have been used to predict species' potential distribution changes at various  
12 478 spatial scales (Pacifi *et al.*, 2015), and have been widely applied to assess climate change  
13 479 vulnerability of plants (Midgley *et al.*, 2002; Thuiller *et al.*, 2005; Fitzpatrick *et al.*, 2008),  
14 480 invertebrates (Harrison *et al.*, 2006; Settele *et al.*, 2008; Heikkinen *et al.*, 2010; Sánchez-Fernández  
15 481 *et al.*, 2011) and vertebrates, including birds (Gregory *et al.*, 2009; Hole *et al.*, 2011; Garcia *et al.*,  
16 482 2012), mammals (Hughes *et al.*, 2012; Songer *et al.*, 2012; Visconti *et al.*, 2015), amphibians (Lawler  
17 483 *et al.*, 2009; Carvalho *et al.*, 2011) and fishes (Jeschke & Strayer, 2008; Yu *et al.*, 2013). We  
18 484 categorise methods for applying the correlative approach as climate envelope, regression-based,  
19 485 machine learning and Bayesian, and describe available tools, data requirements and examples of  
20 486 their application (Supplementary Table 4).  
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22 488 Correlative assessments are very widely used, probably because methods of application are  
23 489 relatively rapid and cost-effective, occurrence data required are easily available for a large number  
24 490 of taxa, and due to their applicability for spatial conservation planning (e.g. Hannah *et al.*, 2002;  
25 491 Araujo *et al.*, 2004; Phillips *et al.*, 2008; Araújo *et al.*, 2011). Choice of modelling technique is one of  
26 492 the major sources of uncertainty in correlative models (Diniz-Filho *et al.*, 2009; Garcia *et al.*, 2012)  
27 493 but valuable guidance on using and understanding correlative models is available, including from  
28 494 (Pearson, 2007; Franklin, 2009; Peterson *et al.*, 2011; Anderson, 2012, 2013). Shortcomings of  
29 495 correlative CCVAs have been widely discussed (e.g. Pearson & Dawson, (2003b), Hijmans & Graham  
30 496 (2006), Hannah *et al.*, (2007), Araújo & Peterson (2012) and Pacifi *et al.*, (2015)); their assumption  
31 497 that species' distributions are in equilibrium with the prevailing climate can prove problematic in  
32 498 cases where a species' contemporary distribution reflects the outcome of recent or historical  
33 499 pressures (e.g. habitat loss, persecution) or natural dispersal barriers that have excluded the species  
34 500 from areas of suitable climate (Guisan & Thuiller, 2005). Other challenges include poor performance  
35 501 for species with few records (see section below on 'Species that pose particular CCVA challenges'),  
36 502 failure to account for local adaptation, and difficulty in projecting suitability for novel climatic  
37 503 conditions (i.e. outside the climatic range of the training data).  
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39 505 When validated using species' observed responses to recent climate changes, however, correlative  
40 506 CCVAs have been shown to perform well in predicting species' population increases/decreases in  
41 507 many cases (Green *et al.*, 2008; Gregory *et al.*, 2009; Stephens *et al.*, 2016) and to have a fair ability  
42 508 to predict distribution changes (e.g. Chen *et al.*, 2011; Dobrowski *et al.*, 2011; Morelli *et al.*, 2012;  
43 509 Smith, 2013). The range of potential impact mechanisms may be increased, for example, by  
44 510 incorporating variables such as inter-species interactions (e.g. Schweiger *et al.*, 2008, 2012), the

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3 511 availability of nesting sites (e.g. Heikkinen *et al.*, 2007) and habitat shifts (e.g. Thuiller *et al.*, 2006a)  
4 512 along with climate variables in models. Further advances are being made by combining correlative  
5 513 and trait-based approaches, including by incorporating estimates of dispersal ability (e.g. Warren *et al.*,  
6 514 2013) and sensitivity and adaptive capacity (e.g. Garcia *et al.*, 2014a) into projections of species'  
7 515 range shifts (see 'Combined approach' and 'Improving CCVA methodology' below).  
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10 517 *Inferring distribution changes from model projections*  
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13 519 Most correlative models output continuous values of 'suitability' or probability of occurrence of a  
14 520 species for each grid cell, generally requiring assessors to select a threshold value separating species  
15 521 'presence' from 'absence' in order to estimate potential changes in the species' distribution.  
16 522 Threshold values are typically determined as those which optimise model goodness-of-fit. However,  
17 523 as Liu *et al.* (2005, 2013) showed, different measures of goodness-of-fit can give very different  
18 524 threshold values, with the True Skill Statistic (Allouche *et al.*, 2006) emerging as the most robust  
19 525 measure for this purpose. However, since different thresholds can yield dramatically different  
20 526 conclusions about whether a species' distribution will decrease or expand under climate change  
21 527 (Nenzén & Araújo, 2011), we recommend carefully experimenting with alternative threshold rules  
22 528 with consideration as to whether optimistic or pessimistic outcomes are more appropriate for the  
23 529 analysis. A complement or alternative to thresholding is to use the raw suitability values to assess  
24 530 whether environmental conditions improve or degrade for the species (e.g. Still *et al.*, 2015), i.e.  
25 531 how the 'quality' of the potential area of distribution changes.  
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30 533 *Inferring population changes from distribution changes*  
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34 535 Changes in distribution extent are unlikely to be linearly related to population changes because: (a)  
35 536 individuals are rarely evenly spread throughout a species' overall distribution; (b) suitable habitat  
36 537 patches in areas newly climatically suitable may not be large enough to support viable  
37 538 subpopulations; and (c) dispersal limitations may prevent the species from colonising areas that  
38 539 become newly climatically suitable. These factors are species-specific and must therefore be  
39 540 considered separately for each focal species' CCVA. In the context of IUCN Red Listing, in the  
40 541 absence of more specific information, it is allowable to infer a linear relationship between  
41 542 population and distribution changes (although this should be explicitly stated). Suitability values  
42 543 provide a basis for improving upon such an assumption; even without any change in distribution  
43 544 extent, a decrease in mean suitability indicates a likely population decline. Where abundance data  
44 545 (or a proxy for abundance, e.g. recording rate) are available, these may be used to model the  
45 546 relationship between abundance and bioclimatic variables, hence enabling projections of future  
46 547 abundance patterns which are then more closely linked to measures of future conservation status  
47 548 and extinction risk (e.g. Huntley *et al.*, 2012; Renwick *et al.*, 2012; Johnston *et al.*, 2013; Massimino  
48 549 *et al.*, 2017).  
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3 552 *Mechanistic approach*  
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5 553 Mechanistic assessments use process-based simulation models to quantify climate change impacts,  
6 554 and explicitly incorporate focal mechanisms (Morin & Thuiller, 2009), thereby allowing projection  
7 555 under novel climate conditions. One of two sub-types (Supplementary Table 5), *mechanistic niche*  
8 556 models, project species' future ranges using estimates of species' physiological tolerances, typically  
9 557 from field or laboratory observations (e.g. Jenouvrier *et al.*, 2009; Radchuk *et al.*, 2013; Overgaard *et al.*,  
10 558 2014) or energy balance equations (e.g. Molnár *et al.*, 2010; Huey *et al.*, 2012; Kearney & Porter,  
11 559 2009). Because they estimate species' fundamental niches they may perform poorly in predicting  
12 560 realised niches when species interactions are important, especially when physiological tolerances  
13 561 are measured in the laboratory. Secondly, *demographic* models project changes in abundance,  
14 562 usually through simulating climate change impacts on individuals, subpopulations, or species (e.g.  
15 563 Stanton, 2014; Aiello-Lammens *et al.*, 2015; Heinrichs *et al.*, 2016; Naveda-Rodríguez *et al.*, 2016);  
16 564 they can therefore be used to assess extinction risk (e.g. Keith *et al.*, 2008; Brook *et al.*, 2009;  
17 565 Pearson *et al.*, 2014). However, such models are very data intensive, requiring knowledge of the  
18 566 relationships between a series of demographic parameters (e.g. adult survival, juvenile survival,  
19 567 fecundity) and relevant climate variables. Supplementary Table 5 provides a further classification of  
20 568 mechanistic models, as well as examples of their use.  
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25 570 Mechanistic CCVAs can include a broad range of climate change impact mechanisms, including  
26 571 changes in resource availability (e.g. Mantyka-Pringle *et al.*, 2014; Martin *et al.*, 2015), habitat  
27 572 suitability (e.g. Aiello-Lammens *et al.*, 2011; Forrest *et al.*, 2012), and inter-specific interactions (e.g.  
28 573 Urban *et al.*, 2012; Fordham *et al.*, 2013). They can also accommodate interaction effects of climate  
29 574 change and other pressures (e.g. land-use change; Mantyka-Pringle *et al.* (2014, 2016)), as well as  
30 575 direct mortality in specific but different subpopulations and age classes. Morphological and  
31 576 demographic factors, genetic adaptation and phenotypic plasticity may also be included (e.g. Chevin  
32 577 *et al.*, 2010; Huey *et al.*, 2012). Use of such species trait data in the mechanistic approach is  
33 578 distinguished from that of the Trait-based approach, since the latter relies on assessors' *a priori*  
34 579 assumptions of the links between traits and species' vulnerability, while the Mechanistic approach  
35 580 integrates traits into process-based empirical predictions. However, their often intensive  
36 581 requirements for knowledge and data on species and their systems (Morin & Thuiller, 2009), and  
37 582 hence their relative costliness (Kearney & Porter, 2009; Chevin *et al.*, 2010), have significantly  
38 583 limited their application to date and are likely to do so for the foreseeable future.  
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43 585 *Combined approach*  
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45 586 Combining CCVA approaches such that they draw on the strengths of component approaches  
46 587 provides a valuable opportunity to improve CCVA of species (Willis *et al.*, 2015). The trait-based  
47 588 approach, for example, can draw on correlative assessments to estimate range shift predictions and  
48 589 to understand the climatic variables associated with the species' historical ranges (i.e. a trait-  
49 590 correlative approach)(e.g. Young *et al.*, 2012; Smith *et al.*, 2016). The Correlative approach can draw  
50 591 on the trait-based approach by using dispersal distances (e.g. Schloss *et al.*, 2012; Warren *et al.*,  
51 592 2013, 2018; Visconti *et al.*, 2015), and measures of species' sensitivity and adaptive capacity (e.g.  
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3 593 Garcia *et al.*, 2014a) to improve range shift predictions (i.e. a correlative-trait approach). Correlative  
4 594 and mechanistic approaches may be used in combination to enable inclusion of a range of  
5 595 potentially important variables for predicting the suitability of potential future range, including  
6 596 metapopulation dynamics and environmental processes such as sea level rise, fires and stochasticity  
7 597 (e.g. Keith *et al.*, 2008; Anderson *et al.*, 2009; Midgley *et al.*, 2010; Fordham *et al.*, 2012), as well as  
8 598 inter-species interactions (e.g. Harris *et al.*, 2012; Fordham *et al.*, 2013) (i.e. a correlative-  
9 599 mechanistic approach). Finally, all three approaches may be combined in Criteria-based assessments  
10 600 in which species are classified into categories of risk based on the information from correlative  
11 601 and/or mechanistic assessments, species trait data and observed species changes (e.g. Thomas *et*  
12 602 *al.*, 2011) (i.e. a correlative-mechanistic-trait Approach). We provide further details of combined  
13 603 approaches, including data requirements, available tools and examples of their application  
14 604 (Supplementary Table 6), and discuss their potential for advancing CCVA of species under 'Future  
15 605 directions'.  
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### 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 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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3 634 with varying land-surface properties), but the associated increase in computational demands as  
4 635 grain size reduces typically poses a practical limit. At resolutions >20km, species' abundance and  
5 636 distributions can generally be explained by bioclimatic variables alone (Luoto *et al.*, 2007), but at  
6 637 finer scales variables related to habitat suitability, land use and management become important,  
7 638 and below 1 km microclimate becomes dominant. In the latter case, microclimate influences should  
8 639 be explored taking into account factors such as slope, aspect, vegetation and shading by adjacent  
9 640 areas at higher elevation (see e.g. Bennie *et al.*, 2008, 2013; Gillingham *et al.*, 2012; Hodgson *et al.*,  
10 641 2015). At almost all grain sizes relevant to CCVAs important issues that arise with respect to  
11 642 downscaling climate model outputs should be considered (Baker *et al.*, 2017).  
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## 15 644 **Species data**

### 16 17 645 *Distributions*

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19 646 For methods that rely on occurrence or locality records to characterise species' bioclimatic  
20 647 tolerances (i.e. correlative modelling approaches), using data of good quality is particularly  
21 648 important. Ideal sources include surveys or atlases, and well-validated specimen and citizen science  
22 649 records. Data from large distribution databases (Supplementary Table 7) provide a convenient  
23 650 source of data but must be carefully reviewed for accuracy. Where available, data on species'  
24 651 abundances (or based on abundance proxies such as reporting rate) are especially valuable. Expert-  
25 652 developed range polygons may be used when they are based on first-hand knowledge of current  
26 653 species occurrence or where gridded data or point records are unavailable, but they are likely to  
27 654 have a higher incidence of false presences (commission errors) especially if patchiness in the species'  
28 655 distribution within polygons is not accounted for.  
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33 657 False presences also arise from species misidentification or taxonomic uncertainty, incorrect locality  
34 658 recording or data entry error, and can lead to overestimation of species' environmental niches. The  
35 659 most common cause of uncertainty, however, is false absences (omission errors). These typically  
36 660 arise from spatial differences in sampling effort (e.g. low sampling effort away from roads, in  
37 661 inaccessible areas, or in countries with limited resources to survey biodiversity), differences in  
38 662 detectability (e.g. fewer records of cryptic species) or in level of interest/charisma (e.g.  
39 663 disproportionate number of records for charismatic species). Some datasets provide data from  
40 664 which detection probability can be estimated (e.g. Southern African Bird Atlas Project (Harrison *et*  
41 665 *al.*, 1997) Breeding Bird Surveys (Massimino *et al.*, 2017) or on areas where the species was sought  
42 666 and not found (e.g. European Bird Census Council Atlas (Hagemeijer & Blair, 1997). For correlative  
43 667 models, Guillera-Arroita *et al.* (2015) provide guidance on how the type of distribution data (and  
44 668 associated sampling bias) determines the quantity that is estimated by the models. Various  
45 669 approaches have been proposed to address spatial biases in species' presence data. Phillips *et al.*,  
46 670 (2009) developed models that use all records of presence for members of a group of species to  
47 671 generate a background sample of pseudo-absences for the focal species that have the same spatial  
48 672 bias as the collective presence records. Other approaches include Bayesian approaches (Manceur &  
49 673 Kühn, 2014; Rocchini *et al.*, 2017), subsampling in geographic space (Aiello-Lammens *et al.*, 2015) or  
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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 (Snober  
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) Which 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.

#### 698 *Bioclimatic variables*

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.

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3 713 Autecological studies identifying precise bioclimatic variables that affect a particular species'  
4 714 performance or survival, and their mechanisms of action, are rare (e.g. Pigott & Huntley, 1981).  
5 715 However, general biological knowledge accumulated for a variety of taxonomic groups and climate  
6 716 regions, assessments of bioclimatic variable performance (e.g. Barbet-Massin & Jetz, 2014) and  
7 717 previous published models provide a basis for an informed choice of bioclimatic variables for most  
8 718 species. Mean annual temperature or precipitation are unlikely ever to be mechanistically important  
9 719 (Bateman *et al.*, 2012; Huntley, 2012; Platts *et al.*, 2013) but coldest and/or warmest month means  
10 720 or annual extremes and annual thermal sums above or below relevant thresholds, for example, have  
11 721 well-understood mechanistic roles for a wide range of taxonomic groups. For higher plants, the  
12 722 balance between precipitation and evaporation is mechanistically relevant, while members of other  
13 723 taxonomic groups may be greatly influenced by the distribution of precipitation through the year.  
14 724 Other taxon-specific measures relating to particular periods of high sensitivity to weather conditions,  
15 725 such as the breeding season (Pearce-Higgins *et al.*, 2015a) may also be considered.  
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20 727 Regionally, for tropical species, relevant bioclimatic variables are likely to include a combination of  
21 728 coldest and warmest month mean temperatures, annual ratio of actual to potential  
22 729 evapotranspiration, the intensity of the dry/wet season, and measures of rainfall bimodality (i.e.,  
23 730 two rainy seasons in a year). For temperate species, the best default bioclimatic variables are likely  
24 731 to include the coldest month mean temperature, annual thermal sum above 5°C, and the annual  
25 732 ratio of actual to potential evapotranspiration. For some cool temperate species that have a 'chilling'  
26 733 requirement, a measure of the length of the period with temperatures below a threshold (e.g. 0°C),  
27 734 or the (negative) annual thermal sum below 0°C can be an important additional variable, as well as  
28 735 snow water equivalent (SWE).  
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32 737 *General Circulation Models (GCMs)*. GCMs are computationally intensive mathematical models of  
33 738 atmosphere and ocean processes that are used to generate weather forecasts and climate change  
34 739 projections. GCM outputs differ due to dissimilarities in the ways that models simplify and simulate  
35 740 *extremely* complex systems, as well as due to knowledge-gaps in climate science. No GCM perfectly  
36 741 reproduces all of the features of the global climate system, so use several models to understand the  
37 742 uncertainties in projections is essential. Fordham *et al.* (2011, 2012) offers some tools for model  
38 743 selection, ensemble building based on model skill, and downscaling. Model inclusion by the IPCC in a  
39 744 recent report (IPCC, 2013) conveys legitimacy, and those selected should reflect the range of  
40 745 uncertainty amongst models by including those that are relatively 'warm', 'cool', 'wet', and 'dry', as  
41 746 well as those whose mean temperature and precipitation projections are near the mean of all  
42 747 models. Models that perform 'best' in the geographical region of interest should be favoured (Baker  
43 748 *et al.*, 2015). Where possible, use of observed climate data to assess model performance under past  
44 749 conditions in CCVA focal areas is also valuable. The IPCC's Data Distribution Centre is a portal for a  
45 750 broad range of GCM outputs.

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49 751 Projections from the individual models selected, collectively referred to as the model 'ensemble',  
50 752 may be averaged to produce a single projection, with the degree of agreement between projections  
51 753 represented by a measure of 'spread' such as the standard deviation or coefficient of variation (for  
52 754 details and caveats of model averaging, see Dormann *et al.* (2018)). While this is often carried out in

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3 755 other contexts, for CCVA this is inadvisable because it provides little insight into the uncertainty of  
4 756 CCVA outputs. Conducting individual assessments using projections from several (at least three)  
5 757 individual models is preferable to a single assessment applied to one model ensemble. Additionally,  
6 758 since different models may generate qualitatively different circulation patterns, averaging them  
7 759 could also result in an ensemble mean projection that is mechanistically unrealistic or physically  
8 760 impossible, or that disguises year-to-year variations that may be important drivers of vulnerability.

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10 762 Where a CCVA's spatial extent is relatively limited, and particularly in areas of complex topography,  
11 763 projections using Regional Climate Models (RCMs (Morales *et al.*, 2007)) are generally more accurate  
12 764 than GCM projections downscaled using change factors or statistical downscaling, because RCMs  
13 765 operate mechanistically on horizontal resolutions of tens rather than hundreds of kilometres. The  
14 766 island of Madagascar, for example, is spanned by only approximately 15 grid cells at a typical GCM  
15 767 resolution, but by over 300 RCM cells (55 km in size). However, it is essential to ensure that the  
16 768 GCM-derived boundary conditions used by the RCM simulation are from an appropriate GCM  
17 769 simulation. The Coordinated Regional Climate Downscaling Experiment (CORDEX) provides a series  
18 770 of regional datasets derived from RCM simulations at continental scale, with a grain size of 0.11 to  
19 771 0.44 decimal degrees (~12 to 49 km at the equator) depending on the model and continent, whilst  
20 772 the Hadley Centre PRECIS RCM can be run using either this grain size or a 25km grid (Jones *et al.*,  
21 773 2004). Where possible, use of the most appropriate regional models that have been shown to  
22 774 provide good predictive performance for the area / variables of interest is advisable (Baker *et al.*,  
23 775 2017). Even regional models, however, are unable to account for fine-scale climate variability across  
24 776 regions with high relief. A subsequent, non-mechanistic, downscaling step may therefore be  
25 777 desirable to recover finer-scale spatial variation at sub-RCM grid scales; the change factor method,  
26 778 for example, involves combining anomalies between modelled current and projected climate  
27 779 variables with those from observed climate datasets at finer scales (see Foden & Young, 2016).

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### 29 781 *Greenhouse Gas Trajectories and Emissions Scenarios*

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31 783 Greenhouse gas trajectories aim to capture the uncertainty in future climate due to different future  
32 784 anthropogenic emissions. The IPCC's Fifth Assessment Report (IPCC, 2014) includes four  
33 785 Representative Concentration Pathways (RCPs) or trajectories: RCP 2.6, RCP 4.5, RCP 6 and RCP 8.5  
34 786 (the radiative forcing in  $W.m^{-2}$  determines the number succeeding RCP), which supersede the SRES  
35 787 scenarios used by the IPCC's third (2001) and fourth (2007) assessments. Selecting trajectories  
36 788 typically involves identifying a broad range of plausible possible futures and may include adoption of  
37 789 the precautionary principle. In support of the latter, evidence from the past 25 years is that  
38 790 emissions have continued more or less along the worst-case trajectory (i.e. 'business-as-usual')  
39 791 considered plausible by the IPCC in 1990 (Raupach *et al.*, 2007). In addition, improvements in climate  
40 792 models over the same period have not reduced the magnitude of disparities between changes  
41 793 projected by different models and under different emissions scenarios, nor have they resulted in any  
42 794 substantial change in the magnitude of projected potential climate changes. If the precautionary  
43 795 principle is adopted, then RCP8.5 is recommended.

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.

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## 812 **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.

## 832 **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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3 835 pressures (Turner *et al.*, 2010, but see Young *et al.*, 2012). Such responses include changing land use  
4 836 (e.g. due to expansion of biofuel plantations, land abandonment, new agricultural demands as  
5 837 people migrate), increased water abstraction and building hard infrastructure (e.g. sea walls, dams,  
6 838 wind and solar energy installations) (Watson, 2014; Segan *et al.*, 2015). The advent of Nature-based  
7 839 Solutions (Kabisch *et al.*, 2016; Nesshöver *et al.*, 2017), however, introduces the likelihood that some  
8 840 human responses will have positive impacts on species. Segan *et al.* (2015) found that the relative  
9 841 vulnerabilities of Southern African bird species changed markedly when potential impacts of climate  
10 842 change on human communities were considered (Supplementary Table 7 includes the resources  
11 843 they used). Although human response pressures are difficult to predict, their inclusion is a priority  
12 844 for future CCVA approaches (Maxwell *et al.*, 2015).

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#### 16 846 **SPECIES THAT POSE PARTICULAR CCVA CHALLENGES**

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19 847 Although CCVA has been widely applied across taxonomic groups (Pacifi *et al.*, 2015), many species  
20 848 are poorly assessed or frequently omitted due to insufficient occurrence, trait or physiological data.  
21 849 We focus here on species that are omitted from assessments, but note that others such as long-  
22 850 distance migrants may face concerning shortcomings in their assessments due to failure to explicitly  
23 851 incorporate migratory connectivity (Small-Lorenz *et al.*, 2013). With the exception of well-studied  
24 852 taxonomic groups, incomplete species coverage in CCVA applications is common. Species omission  
25 853 rates as high as 33% for African vertebrates (Garcia *et al.*, 2012), 42% of 5,200 species across 17 taxa  
26 854 in England, a relatively well-monitored and data-rich country (Pearce-Higgins *et al.*, 2017) and 92%  
27 855 for threatened sub-Saharan amphibians (Platts *et al.*, 2014) mean that general conclusions about  
28 856 species' vulnerability to climate change may be biased toward better-known species (Schwartz *et al.*,  
29 857 2006; Platts *et al.*, 2014). Challenges in the application of conventional CCVA methods arise for three  
30 858 types of species in particular: those that are *poorly-known*, those with *naturally small ranges*, and  
31 859 those with *ranges that have become smaller due to other anthropogenic pressures*. For these species  
32 860 to be included in assessments, enhanced data to allow the use of conventional CCVA methods,  
33 861 modified CCVA methods or alternative approaches are needed.

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38 862 Efforts to fill data gaps and use conventional CCVA methods can rely on inferences from data for  
39 863 related species (Foden *et al.*, 2013), expert opinion (Murray *et al.*, 2009; Martin *et al.*, 2015), data  
40 864 imputation techniques, or a combination of literature and targeted fieldwork (Williams *et al.*, 2009).  
41 865 Conventional CCVA methods can be modified to accommodate incomplete data. Correlative  
42 866 modelling of poorly-known and small-range species can rely on simplified correlative techniques  
43 867 (Hof *et al.*, 2011; Platts *et al.*, 2014), more complex techniques with adjusted parameters (Hof *et al.*,  
44 868 2011), methods that account for potential biases in sampling effort (Beale *et al.*, 2014), or consensus  
45 869 building around several models based on a small number of predictors (Lomba *et al.*, 2010). For  
46 870 declined-range species, correlative models could overestimate climate change vulnerability if, for  
47 871 example, warmer parts of the range have been lost for non-climatic reasons (e.g. deforestation at  
48 872 low elevations); therefore, the extant range should be augmented with information on the historic  
49 873 range whenever possible. Another modification to conventional CCVA methods is to redefine  
50 874 taxonomic focus of the models, selecting either a resource used by the focal species that has

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3 875 sufficient data (Delean *et al.*, 2013), or a species assemblage that includes the focal species.  
4 876 Assemblages can be defined with reference to community types (Ferrier & Guisan, 2006), biomes  
5 877 (Midgley *et al.*, 2003), or shared traits (Golicher *et al.*, 2008; Vale & Brito, 2015) that are thought to  
6 878 mediate species' responses to climate change. Caution is needed, however, in the use of such  
7 879 approaches given the evidence from the Quaternary record of the individualistic responses of  
8 880 species to past climate changes (e.g. Huntley, 1991; Graham *et al.*, 1996) and the resulting  
9 881 impermanence of species assemblages (e.g. Graham & Grimm, 1990; Huntley, 1996).

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12 882 Alternative approaches make use of available data to draw inferences about species' vulnerability to  
13 883 climate change (Table 7). When historical data on population and climate variability are available,  
14 884 temporal analysis can be used to identify long-term trends in potential climate drivers of population  
15 885 change and infer future population changes under projected climates (Pearce-Higgins *et al.*, 2017).  
16 886 When the information available is restricted to climate data, assessments can be based solely on the  
17 887 exposure of geographical areas to climate changes. Analysis of multiple dimensions of climate  
18 888 change, such as velocities of temperature change or the disappearance of specific climate  
19 889 conditions, and associated threats and opportunities for species (Garcia *et al.*, 2014b) can provide  
20 890 indications of the likely vulnerability of species present in such areas (Ohlemuller *et al.*, 2008; Garcia  
21 891 *et al.*, 2014a).  
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*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)
<b>Conventional approaches</b>			
<b>Correlative models</b>	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
<b>Mechanistic models</b>	Problematic where mechanistic information is insufficient	Applicable if mechanistic data available	Applicable if mechanistic data available
<b>Trait-based models</b>	Problematic where trait information is insufficient	Applicable if trait data available	Applicable if trait data available
<b>Alternative approaches</b>			
<b>i. Fill data gaps</b>	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
<b>ii. Temporal analysis of population variability</b>	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.
<b>iii. Modified correlative</b>	Potentially applicable; advantageous when	Potentially applicable, and advantageous	Potentially applicable, but important to

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5	<b>techniques</b>	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
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8	<b>iv. Alternative taxonomic focus</b>	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
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19	<b>v. Exposure assessment of geographic area</b>	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.

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

Assessment stage and approach	Relevant Red List parameters
<b>Stage 1:</b> Expert and trait-based assessment	<ul style="list-style-type: none"> <li>• Very restricted distribution and the plausibility and immediacy of threat (D2)</li> <li>• Number of locations (B, D2)</li> <li>• Severe fragmentation (B, C2)</li> <li>• Extreme fluctuations (B, C2)</li> <li>• Continuing decline (B, C2)</li> <li>• <i>Suspected</i> population reduction (A)</li> </ul>
<b>Stage 2:</b> Correlative assessment and correlative-trait combinations	<ul style="list-style-type: none"> <li>• Estimated continuing decline (C1)</li> <li>• <i>Inferred</i> or <i>projected</i> population reduction (A)</li> </ul>
<b>Stage 3:</b> Mechanistic assessment and mechanistic-correlative-trait combinations	<ul style="list-style-type: none"> <li>• Estimated continuing decline (C1)</li> <li>• <i>Projected</i> population reduction (A)</li> <li>• Probability of extinction (E)</li> </ul>

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3 915 **FUTURE DIRECTIONS**

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5 916 **CCVA validation**

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7 917 Validation of CCVAs is an important process that identifies how well the different methods are  
8 918 performing. This is crucial both for understanding uncertainty in current assessments and for guiding  
9 919 model choice and development for future assessments. Comparisons of the results of different  
10 920 CCVAs have highlighted variable results when considering the same species (Lankford *et al.*, 2014;  
11 921 Wheatley *et al.*, 2017), so identifying which approaches are most effective is essential to aid  
12 922 conservation practitioners and policy makers when making decisions based on the CCVA outputs.

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15 924 Most of the approaches applied to CCVA validation to date have been focussed on the performance  
16 925 of ecological niche models and similar correlative methods, testing model-based predictions across  
17 926 space and through time. The most commonly used approach involves repeatedly fitting models using  
18 927 randomly selected subsets of the available data from a single time period (e.g. 70% of the records),  
19 928 with performance of the model assessed on how well the remaining data are predicted by them  
20 929 (Araújo *et al.* 2005; Pearson *et al.*, 2007; Hole *et al.*, 2009; Araújo *et al.*, 2011; Garcia *et al.*, 2012).  
21 930 However, this can lead to an overestimation of predictive ability, because data in the test set are  
22 931 spatially autocorrelated with those used for calibration (Beale *et al.*, 2008). Where possible, it is  
23 932 preferable to predict a species' distribution in one geographic region based on a model fitted to  
24 933 records from a different region (Beerling *et al.*, 1995; Randin *et al.*, 2006), again comparing the  
25 934 predicted distribution with the actual distribution data for the non-modelled region to assess how  
26 935 well the model has performed. Alternatively, geographic partitioning of the study area can generate  
27 936 validation data that are more spatially independent than data resulting from random sub-setting  
28 937 (Morueta-Holme *et al.*, 2010; Wenger & Olden, 2012). In this case, the study area is divided into  
29 938 distinct geographic sections, such as spatially clustered tiles or longitudinal bands, and the model is  
30 939 fitted and evaluated with records from distinct sections.

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33 941 Both of these approaches (random subsets and 'out of area') only consider model performance  
34 942 during the same timeframe, which may be of limited applicability for a model that is designed to  
35 943 assess temporal changes in response to climate change. One way to improve this is to use the model  
36 944 to predict distribution in another time period (either forward or backwards in time; Hill *et al.*, 1999;  
37 945 Araújo *et al.*, 2005; Morelli *et al.*, 2012; Bled *et al.*, 2013; Watling *et al.*, 2013; Huntley *et al.*, 2014).  
38 946 The model predictions can then be tested against actual records in the non-modelled time period or,  
39 947 most rigorously of all, tested against changes to the distribution or abundance either forwards or  
40 948 backwards through time (Green *et al.*, 2008; Gregory *et al.*, 2009; Illan *et al.*, 2014; Stephens *et al.*  
41 949 2016). Such tests have demonstrated that correlative methods can have useful predictive power  
42 950 when modelling changes in distribution or abundance, and therefore may be informative when  
43 951 predicting species vulnerability under climate change.

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46 953 Combined CCVAs incorporate different (depending on the specific method) types of information  
47 954 about the attributes of species, environments they occupy, and their empirical population and  
48 955 distribution trends, as well as correlative model-based projections. There has been relatively little

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3 956 validation of trait-based CCVAs, although it is possible to do so by comparing results of the  
4 957 assessment for a species against observed changes in that species' distribution or abundance under  
5 958 climate change (where available). One recent study (Wheatley *et al.*, 2017) using this approach  
6 959 found that trait-only CCVAs did not predict changes in status through time successfully whereas  
7 960 methods that included population and/or distribution trends (incorporating correlative projections)  
8 961 as well as some trait information (e.g. habitat and dispersal constraints) could predict changes in  
9 962 status. This validation was limited to one geographic region over a relatively short time period, so  
10 963 further work is required to broaden the scope of CCVA validation and establish which methods work  
11 964 best under different circumstances.

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### 13 966 **Improving biodiversity data**

14 967 The absence of readily available, research-quality data on species' distributions, physiological  
15 968 tolerances, interspecific interactions and ecological traits limits the application of CCVA methods for  
16 969 many species, especially those in non-charismatic groups and/or poorly-studied regions (Foden *et al.*,  
17 970 2013; Butt *et al.*, 2016; Supplementary Table 7). The poor coordination and disharmony of  
18 971 existing biodiversity observations are additional challenges (Scholes *et al.*, 2012; Joppa *et al.*, 2016).  
19 972 Increasing the quantity, quality and coordination of biodiversity data is therefore a priority to allow  
20 973 application of CCVA methods to more species, validate CCVA outputs, enable more widespread use  
21 974 of mechanistic models and perform the monitoring needed to integrate climate change adaptation  
22 975 into conservation plans and actions. Furthermore, recognition of the value of trait variability in  
23 976 addition to species means will improve predication accuracy (Cordlandwehr *et al.*, 2013).  
24 977 Encouraging signs are the increasing availability of digital locality data through portals such as the  
25 978 Global Biodiversity Information Facility, published trait databases (e.g. Oliveira *et al.*, 2017), and  
26 979 citizen science schemes for sharing observational data (e.g. eBird, iNaturalist (Pearce-Higgins *et al.*,  
27 980 2018). Progress towards imputing unknown trait data also helps fill data gaps (Penone *et al.*, 2014;  
28 981 Schrodte *et al.*, 2015).

### 29 982 **Advancing CCVA methodology**

30 983 CCVA methodological development remains a fertile area of research. Combined or 'hybrid' methods  
31 984 that draw on the strengths of the three approaches provide much promise. Inter-species  
32 985 interactions are seldom explicitly considered in CCVAs, yet they can be important drivers of climate  
33 986 change impacts on species (Ockendon *et al.*, 2014); Schweiger *et al.* (2008, 2012) and Singer *et al.*,  
34 987 (2018) provide notable exceptions and illustrate how such interactions may be included. Modelling  
35 988 the dynamics of predator-prey, host-parasite and competitor dynamics (including those involving  
36 989 invasive alien species) into the future represents a key gap and challenge. Better understanding of  
37 990 how climate and non-climate pressures interact, and how to account for this interaction in CCVA  
38 991 methods is another challenge (Segan *et al.*, 2015). Greater attention to baselines, and accounting for  
39 992 climate change that has already taken place (IPCC, 2013; van Wilgen *et al.*, 2015; Huntley *et al.* 2018)  
40 993 are needed to improve correlative approaches, especially for species with slow or lagged responses  
41 994 to ongoing climate change. Trait-based models can be improved through better empirical data on

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3 995 thresholds associated with vulnerability for traits. As mentioned, incorporating the effects of human  
4 996 responses to climate change into CCVAs is another area that requires additional development.

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6 997 *Better consideration of climate extremes and variability*

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8 998 Future climates will have more variability and more frequent extreme events, although to date these  
9 999 remain poorly projected by earth system models. Nonetheless, together these will likely have  
10 1000 greater effects on ecological systems than shifts in means alone (Thompson *et al.*, 2013). Extreme  
11 1001 events are challenging to evaluate due to their rarity. Ameca y Juárez *et al.* (2013) analysed impacts  
12 1002 of cyclones and droughts on terrestrial mammals, and Thompson *et al.* (2013) proposed a method  
13 1003 for using downscaled climate projections that incorporate changes in climate variability. Despite the  
14 1004 important roles that variability and extremes play in determining patterns of biological diversity, the  
15 1005 ecology and conservation communities are just beginning to address the impacts of catastrophic  
16 1006 events (Butt *et al.*, 2016; Palmer *et al.* 2017).

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20 1007 **Incorporating molecular information**

21 1008 Molecular data can help in CCVA analyses by providing information on population processes such as  
22 1009 modes of reproduction, past and current dispersal patterns, and changes in population size.  
23 1010 Molecular analyses have traditionally involved microsatellite (=SSR) markers consisting of variation  
24 1011 in the number of short tandem repeats ('microsatellites') at various locations in an organism's DNA,  
25 1012 as well as sequence variation in mitochondrial (mt) and chloroplast (cp) DNA. However, in recent  
26 1013 years there has been a rapid shift from scoring variation in a few (10-30) microsatellite markers to  
27 1014 using thousands of SNP (single nucleotide polymorphism) markers across genomes, since new  
28 1015 sequencing technologies mean that these can now be screened cheaply using non-invasive sampling  
29 1016 (Allendorf, 2017). SNP markers provide a more detailed and accurate picture of population  
30 1017 processes (Çilingir *et al.*, 2017; Younger *et al.*, 2017), including the way in which populations have  
31 1018 expanded and shrunk historically, and their interactions with other populations. Molecular markers  
32 1019 indicate whether ongoing exchange of genes across populations or species has occurred which may  
33 1020 bolster the species' adaptive capacity (Garcia-Elfring *et al.*, 2017).

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38 1021 As information on the genomics and transcriptomics of many groups of organisms increases,  
39 1022 molecular SNP markers are increasingly being used to test for local adaptation across species ranges  
40 1023 (Hoffmann *et al.*, 2015; Allendorf, 2017). Such tests have traditionally relied on controlled  
41 1024 experiments in which populations from different environments are reared under common  
42 1025 conditions and/or translocated between sites; these tests are difficult and time-consuming to  
43 1026 undertake for long-lived species and may not deliver results in a sufficiently timely manner,  
44 1027 particularly for already-threatened species. However, local adaptation to different climates can also  
45 1028 be identified by testing whether genomic markers are correlated with environmental gradients (e.g.  
46 1029 Steane *et al.*, 2014; Schweizer *et al.*, 2016; Harrisson *et al.*, 2017), which in turn can be used to  
47 1030 predict whether gene pool mixing can bolster adaptive capacity (He *et al.*, 2016; Jordan *et al.*, 2017).  
48 1031 Molecular data can also be combined with phenotypic information on species to determine whether  
49 1032 translocations to boost natural populations are successful at increasing fitness (Christmas *et al.*,

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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**CONCLUSION**

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

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

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

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

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3 1107 change. Lastly, we discuss developments in molecular biology and their potential application for  
4 1108 improving CCVA of species.

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6 1109 As change to Earth's climates accelerates, managers and policy makers must become increasingly  
7 1110 informed by CCVAs. The current strategic goals for biodiversity set by the Convention on Biological  
8 1111 Diversity expire in 2020 and largely ignore climate change. To be effective, the post 2020 biodiversity  
9 1112 agenda will need to be more explicit on protecting biodiversity under climate change, thus elevating  
10 1113 the role of CCVA and requiring even more rigor in its application.

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19 1117 **FURTHER READING**

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21 1118 **Resources for climate change adaptation and vulnerability assessment**

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24 1120 • IUCN Species Survival Commission: Guidelines for Assessing Species' Vulnerability to Climate  
25 1121 Change (Foden & Young, 2016)
- 26 1122 • Responding to Climate Change: Guidance for Protected Area Managers and Planners. Developed  
27 1123 by the IUCN World Commission on Protected Areas (Gross *et al.*, 2016).
- 28 1124 • Climate-Smart Conservation: Putting Adaptation Principles into Practice. Developed by the US  
29 1125 National Wildlife Federation (Stein *et al.*, 2014).
- 30 1126 • Climate Change Vulnerability Assessment for Natural Resources Management: Toolbox of  
31 1127 Methods with Case Studies. Developed by the US Fish and Wildlife Service (Johnson, 2014).
- 32 1128 • The Adaptation for Conservation Targets (ACT) Framework: A Tool for Incorporating Climate  
33 1129 Change into Natural Resource Management (Cross *et al.*, 2012, 2013).
- 34 1130 • Scanning the Conservation Horizon: A Guide to Climate Change Vulnerability Assessment.  
35 1131 Developed by a workgroup of US government, non-profit, and academic institutions (Glick *et al.*,  
36 1132 2011).
- 37 1133 • Climate Change and Conservation: A Primer for Assessing Impacts and Advancing Ecosystem-  
38 1134 based Adaptation in The Nature Conservancy (Groves *et al.*, 2010).
- 39 1135 • Voluntary guidance for states to incorporate climate change into state wildlife action plans and  
40 1136 other management plans. Developed by the Association of Fish and Wildlife Agencies  
41 1137 (Association of Fish and Wildlife Agencies, 2009).
- 42 1138 • Species' Distribution Modeling for Conservation Educators and Practitioners (Pearson, 2007).
- 43 1139 • Habitat Suitability and Distribution Models (Guisan *et al.*, 2017).
- 44 1140 • Online Open Course in Species Distribution Modeling (Huijbers *et al.*, 2016).
- 45 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]

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1147 **Sidebar title:**

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

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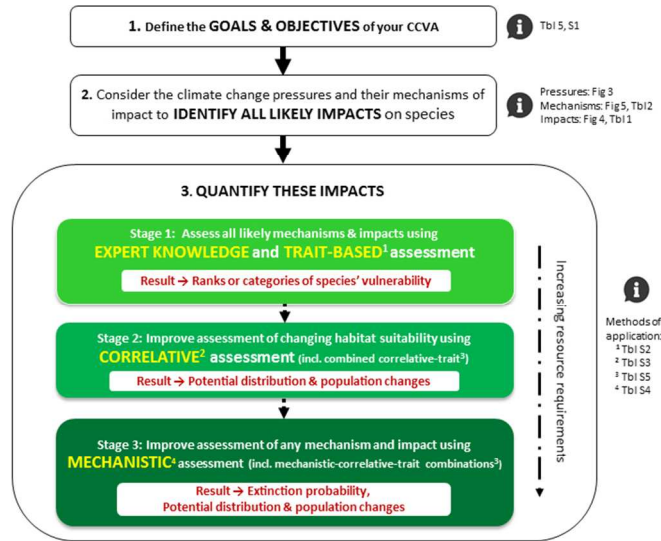
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### STEPS FOR CARRYING OUT CLIMATE CHANGE VULNERABILITY ASSESSMENT OF SPECIES



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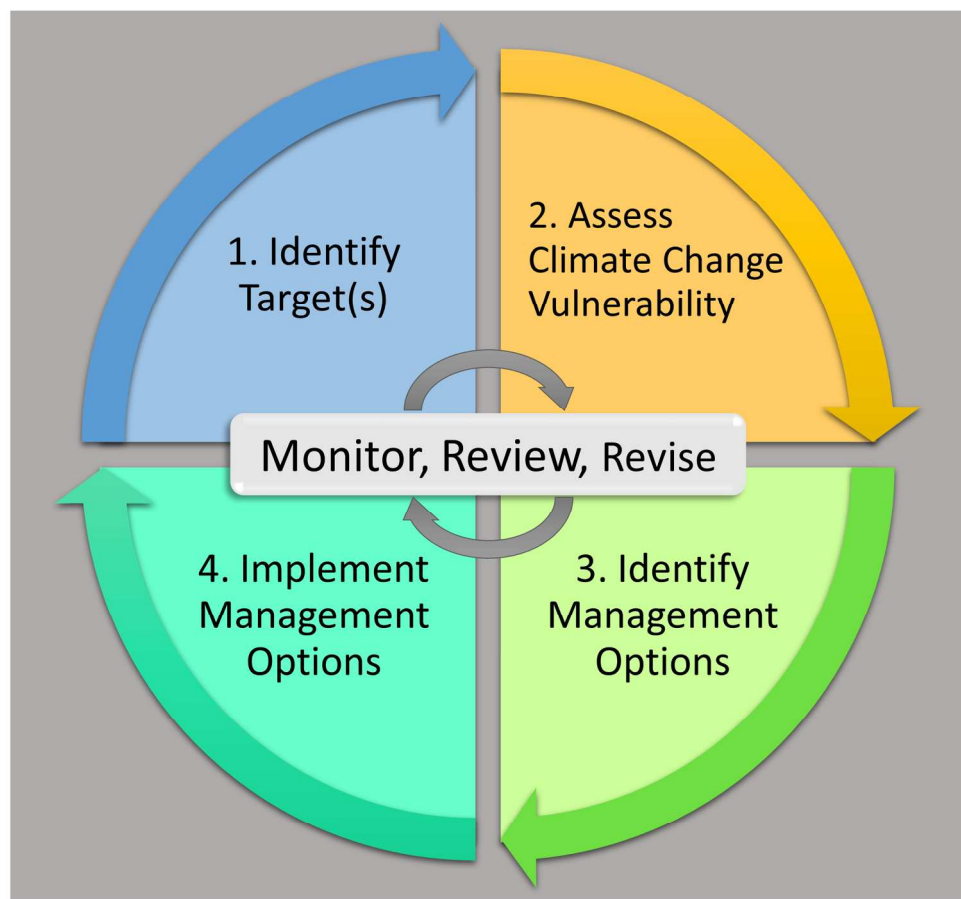


Figure 1: Steps for developing climate change adaptation strategies (Adapted from Glick et al. (2011))

174x162mm (300 x 300 DPI)

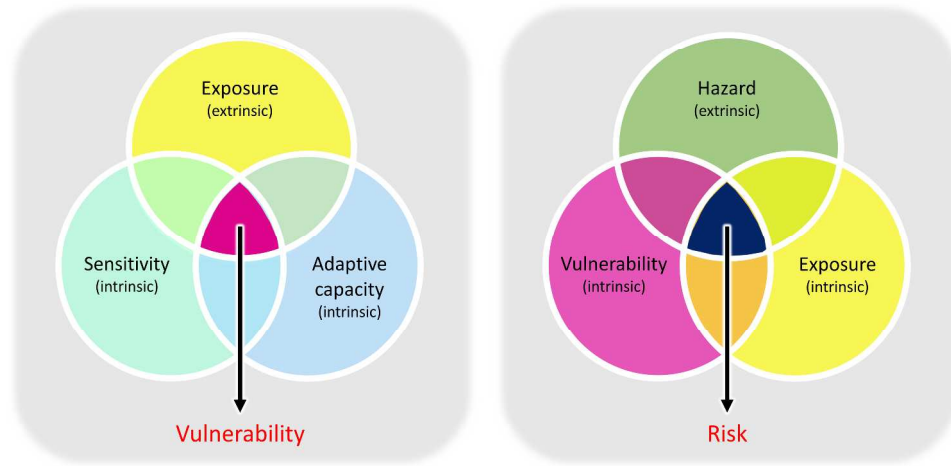


Figure 2a. According to the IPCC Fourth Assessment (2007) and common usage in the field of CCVA of species, vulnerability to climate change results from the interaction of exposure and sensitivity with adaptive capacity (adapted from IPCC, 2007).

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)).

338x190mm (300 x 300 DPI)

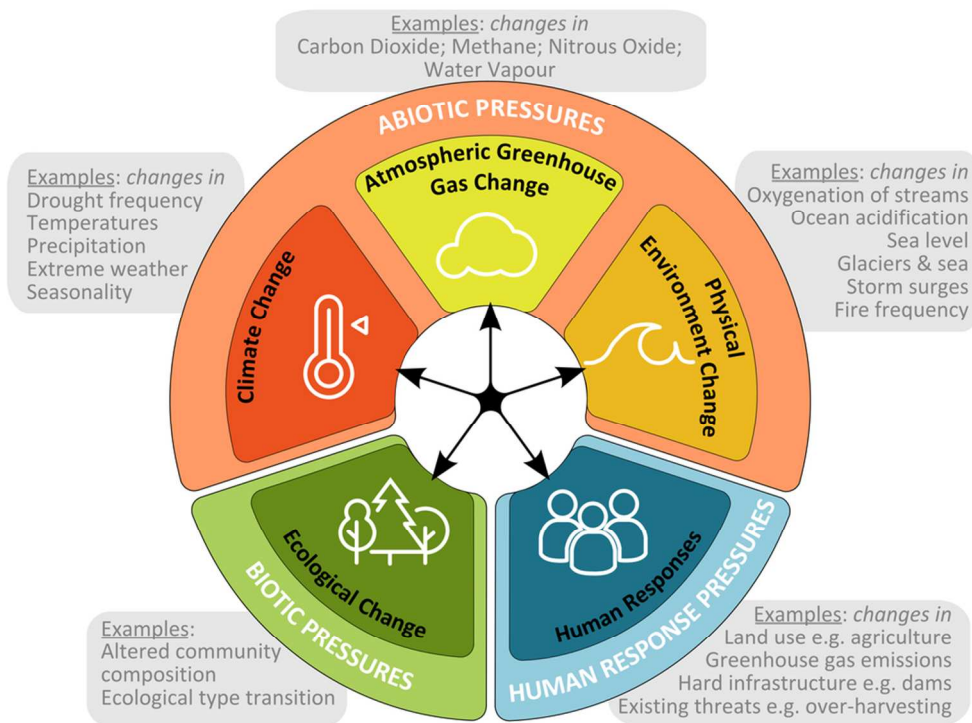


Figure 3. Climate change related pressures on species, showing those originating from abiotic, biotic and human response causes.

92x68mm (300 x 300 DPI)

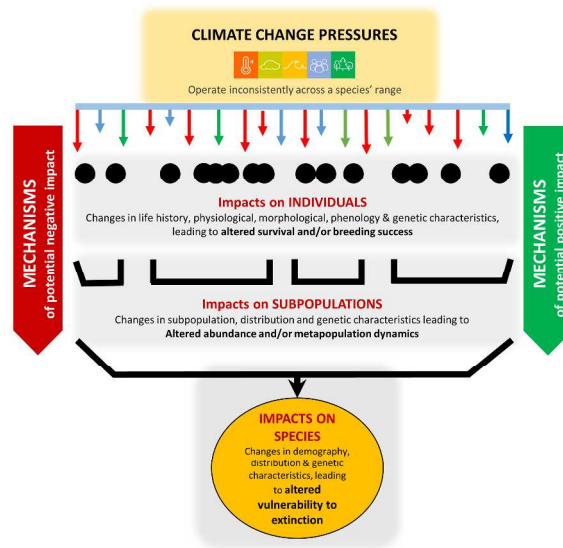


Figure 4. Potential climate change impacts on species include the species-level population and range changes that underpin extinction risk. These changes are driven by changes at individual and subpopulation levels.

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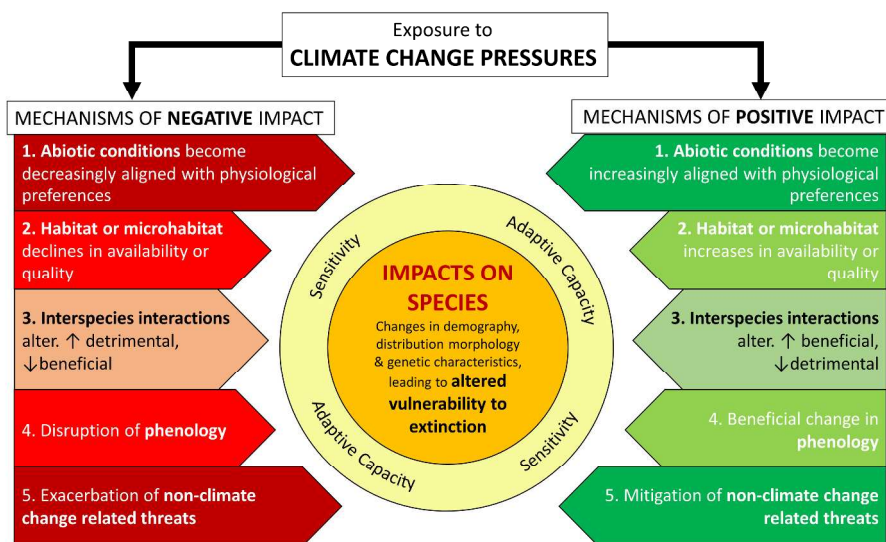


Figure 5. Mechanisms describe the pathways through which climate change pressures may exert impacts on species. These impacts may have positive and/or negative impacts on the species and are mitigated or exacerbated by species' individual sensitivities and adaptive capacities.

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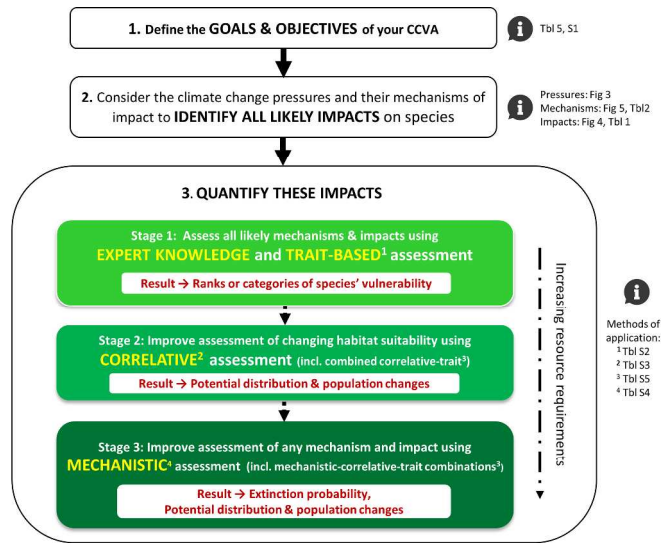


Figure 6. The approaches used to carry out each of the three assessment types and the metrics or types of information of climate change vulnerability that they may produce.

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