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# Climate change vulnerability assessment of species

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# CLIMATE CHANGE VULNERABILITY ASSESSMENT OF SPECIES

Article Type: Overview

**Authors:**

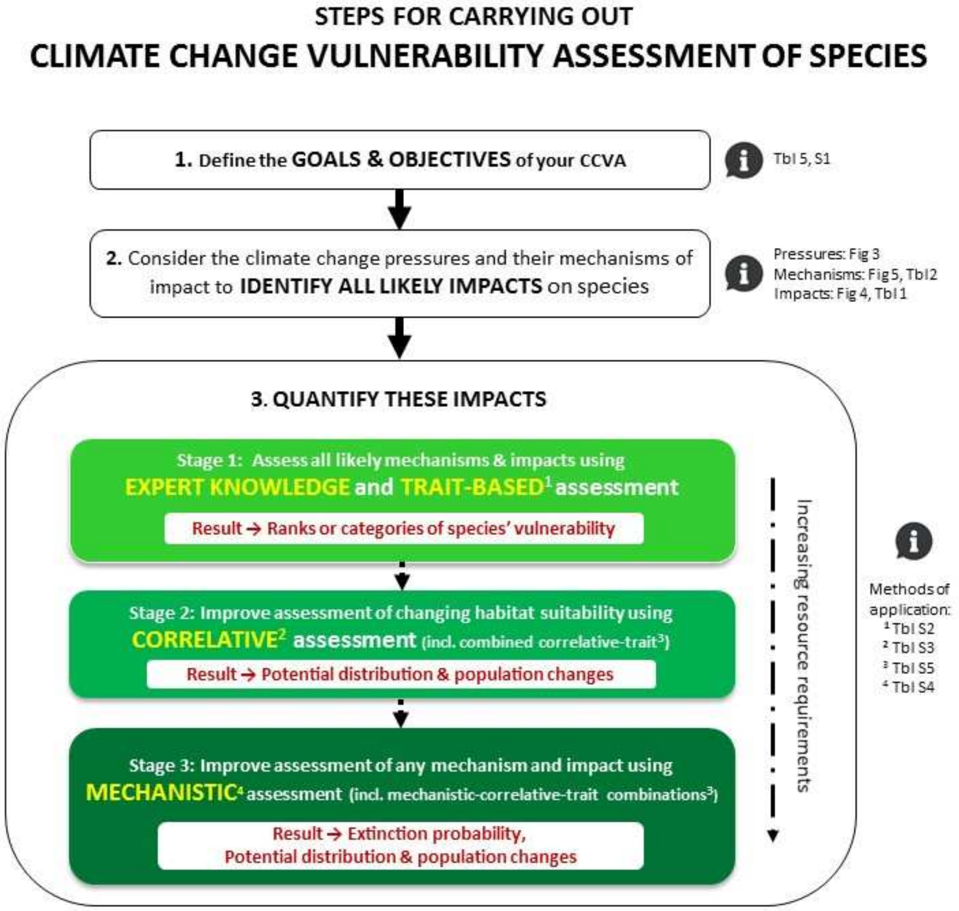
Wendy B. Foden*, Bruce E. Young, H. Resit Akçakaya, Raquel A. Garcia, Ary Hoffman, Bruce A. Stein, Chris D. Thomas, Christopher J. Wheatley, David Bickford, Jamie A. Carr, David Hole, Tara Martin, Michela Pacifici, James W. Pearce-Higgins, Philip J. Platts, Piero Visconti, James Watson and Brian Huntley

*Corresponding Author

## 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.

## GRAPHICAL/VISUAL ABSTRACT



**Caption:**

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

## INTRODUCTION

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

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

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

Over the past decade interest in assessing the climate change vulnerability of biodiversity has increased explosively among managers, planners, policy makers, and researchers working at local, regional and global scales. Nonetheless, predicting climate change impacts on biodiversity remains a major challenge to science (Pereira *et al*., 2010; Pacifici *et al*., 2015), and studies comparing assessments with observed changes have met with limited success (Wheatley *et al*., 2017). Further research is required. This review responds to the proliferation of literature on individual species assessments that predominate over assessments at other biological scales. Based on a collective effort to develop practical, user-friendly guidance for CCVA of species (Foden & Young, 2016), we share key concepts, and guide readers through commonly-used concepts and terms, steps for carrying out assessments, and selecting methods, as well as approaches for communicating and applying results. We outline resources available for users seeking more detailed or specific guidance. Finally, we discuss use of the results in Red List assessments of extinction risk, as well as promising new directions in this rapidly developing field. Since CCVA ultimately feeds into the wider context of identifying leverage points for minimising negative impacts of the climate change crisis on biodiversity (Figure 1), we consistently draw readers' attention back to this conservation context. Vulnerability assessment is primarily about identifying potential problems that must be planned for and addressed by appropriate environmental and conservation policies and actions.

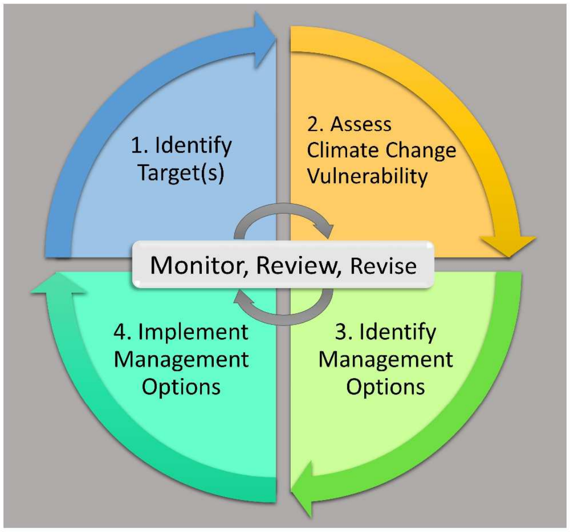


*Figure 1: Steps for developing climate change adaptation strategies (Adapted from Glick et al. (2011))*

## THE EMERGENCE OF CLIMATE CHANGE VULNERABIILITY ASSESSMENT

Although the influence of the atmospheric concentration of carbon dioxide on global climate had been identified already in the late 19th century (Arrhenius, 1896), it was only during the late 1970s that concern about human impacts upon the climate system really began to grow. This concern grew rapidly such that by the mid-1980s there was a steady flow of scientific publications, including such landmarks as the SCOPE 29 volume (Bolin *et al*., 1986) that addressed the potential impacts upon ecosystems both of projected climate changes and of the direct effects of increasing carbon dioxide concentration. In 1987 the International Council of Scientific Unions established the International Geosphere–Biosphere Programme that stimulated international research organised around six core projects, including ‘Global Change and Terrestrial Ecosystems’, and that led to numerous influential publications (e.g. Walker & Steffen, 1996). The rapid growth in international concern also led to the establishment in 1988 of the Intergovernmental Panel on Climate Change (IPCC) that produced its first report in 1990 in which it discussed, albeit briefly, the potential impacts upon biodiversity and identified the potentially most vulnerable ecosystems (Street *et al*., 1990). The implications for conventional approaches to biodiversity conservation began to be discussed around the same time (e.g. Hunter, Jacobson, & Webb, 1988; Huntley & Webb III, 1988) and the lessons that could be learned from studies of Quaternary palaeoecology also began to be discussed (e.g. Huntley & Webb III, 1988; Huntley, 1990, 1991). Subsequently the volume edited by Peters & Lovejoy (1992) represented a key milestone on the road towards formalised assessments of species’ vulnerabilities to climate changes.

Climate change vulnerability assessment as a field emerged in the 1990s, drawing on several disparate disciplinary traditions, including natural hazard and disaster planning, climate change effects research, and endangered species conservation. The concepts behind vulnerability were originally and most fully developed in relation to risks from natural hazards to people and communities. Indeed, the field of climate adaptation has been heavily influenced by the work of such natural hazards researchers as Gilbert F. White and colleagues, who emphasized the importance of social and technological ‘adjustments’ to these hazards (Burton *et al*., 1993). Building on such disaster-related usage, early applications of vulnerability assessment in a climate change context primarily focused on susceptibility of people, infrastructure and economies to harm (Dow, 1992; IPCC, 1996). Adger (2006) offered perhaps the most influential distillation of climate change vulnerability in a socioecological context, noting that ‘the key parameters of vulnerability are the stress to which a system is exposed, its sensitivity, and its adaptive capacity.’

Biogeographers, ecologists and conservation biologists began to explore the potential impacts of climate change on species and ecosystems during the early and mid-1990s (e.g. Lindenmayer *et al.*, 1991; Huntley *et al.*, 1995; Sykes & Prentice, 1995; Sykes *et al.*, 1996). Around the same time observed effects of climate change on species’ distributions began to be documented (e.g. Grabherr *et al*., 1994; Parmesan, 1996; Parmesan *et al*., 1999) and the interacting effects upon species of climate change and habitat availability were discussed (e.g. Hill *et al*., 1999). By the early 2000s, a range of effects of climate change on species was being widely documented (e.g. Hughes, 2000; Parmesan & Yohe, 2003), leading to more explicit interest in determining ‘which species, habitats and regions are most at risk from climate change’ (Pearson & Dawson, 2003), and the realisation that substantial numbers of species could be at risk of extinction (Thomas *et al*., 2004). This in turn led to the application and modification of existing vulnerability frameworks (e.g. Schroter *et al.*, 2005; Adger, 2006) for assessing natural systems, including plant and animal species (Williams *et al*., 2008; Pacifici *et al*., 2018). Such applications were also informed by the rich tradition of assessing species' extinction risk (e.g. the IUCN Red List (Mace & Lande, 1991)) and efforts to integrate knowledge about interacting threats to species persistence.

**Vulnerability**

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

### *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)** |
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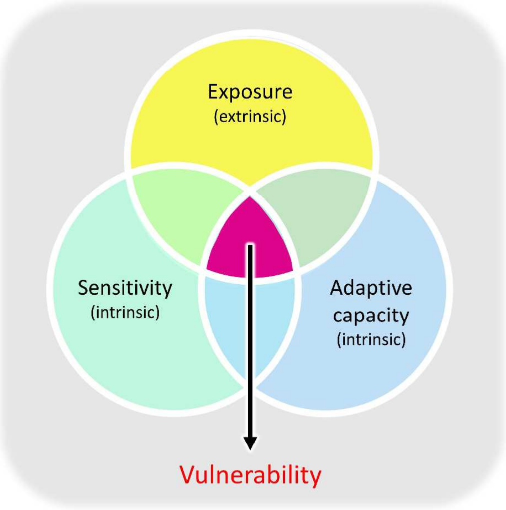
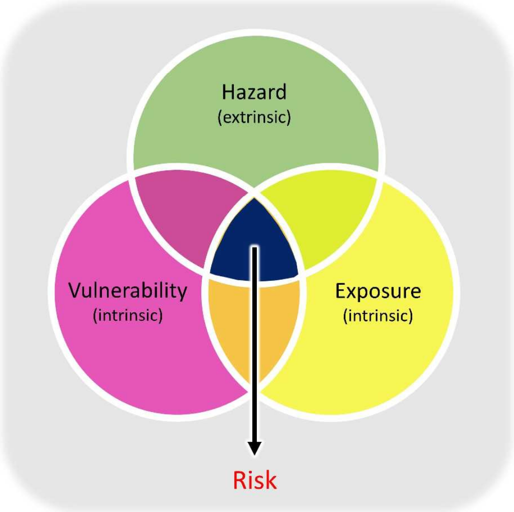
|  <br>*Figure 2a. According to the IPCC Fourth Assessment (2007) and common usage in the field of CCVA of species, vulnerability to climate change results from the interaction of exposure and sensitivity with adaptive capacity (adapted from* IPCC, 2007*).* |  <br>*Figure 2b. According to the IPCC Fifth Assessment (2014), risk of climate-related impacts results from the interaction of climate-related hazards with the vulnerability and exposure of human and natural systems (adapted from IPCC (2014)).* |
| **Overarching measures of concern** | |
| Vulnerability. The extent to which biodiversity is susceptible to or unable to cope with the adverse effects of climate change. It is a function of the character, magnitude and rate of climate change to which the system is **exposed**, its **sensitivity** and its **adaptive capacity** (IPCC, 2007) *(Differs from IPCC, 2014a).* | Risk. The probability of harmful consequences resulting from climate change. Risk results from the interaction of **vulnerability, exposure,** and **hazard**. Risk is often represented as *probability* of occurrence of hazardous events or trends multiplied by the *impacts* if these events or trends occur (IPCC, 2014) *(not defined in 2007)*<br><br>Impact. The effects, consequences or outcomes of climate change on natural and human systems. It is a function of the interactions between climate changes or **hazardous** climate events occurring within a specific time period and the **vulnerability** of an **exposed** society or system (IPCC, 2014) (*Differs from IPCC, 2007*) |
| **Intrinsic Contributing Factors** | |
| Sensitivity. Sensitivity is the degree to which a system is affected, either adversely or beneficially, by *climate variability* or change (IPCC, 2007, 2014)<br><br>Adaptive Capacity. The potential, capability, or ability of a species, ecosystem or human system to adjust to | Vulnerability. 'The propensity or predisposition to be adversely affected. In this usage, vulnerability encompasses a variety of concepts, particularly **sensitivity** to harm and **lack of capacity to cope and adapt.'** (IPCC, 2014) *(Differs from IPCC, 2007).* |

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

**Exposure**

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

*Drivers* are the highest order phenomena governing change; they typically encompass societal demands or needs (e.g. economic, social, and political) and natural factors that are independent of anthropogenic causes (e.g. earthquakes, tectonic drift) (Maxim *et al*., 2009; Oesterwind *et al*., 2016). A key characteristic of drivers is that they are beyond direct control or management (Oesterwind *et al*., 2016). In the context of climate change and biodiversity, drivers are the factors leading to greenhouse gas emissions, including society’s needs for energy, transport and food, as well as contributing natural factors such as volcanic eruptions.

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

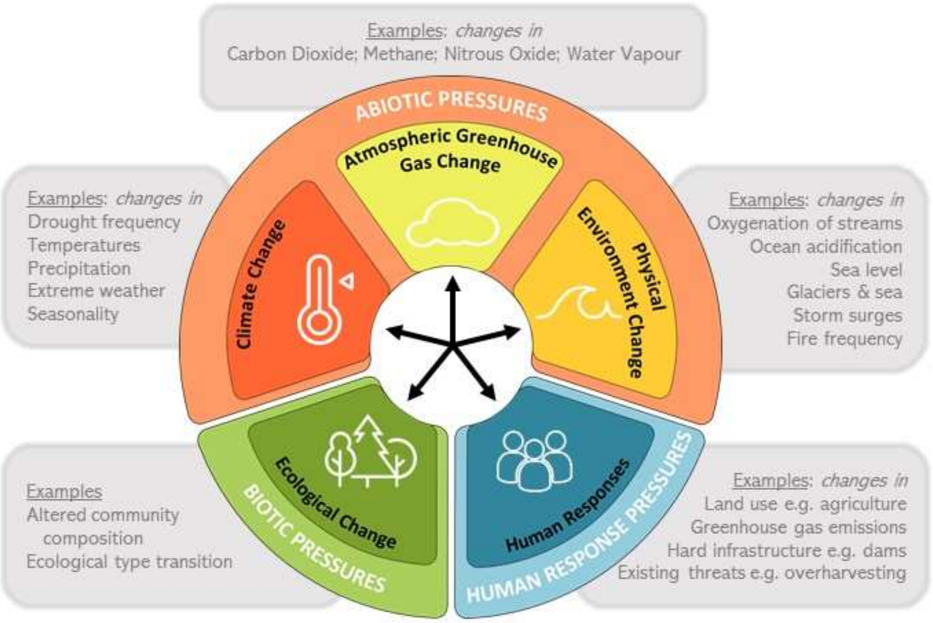

*Figure 3. Climate change related pressures on species, showing those originating from abiotic, biotic and human response causes.*

## Potential impacts and their mechanisms

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

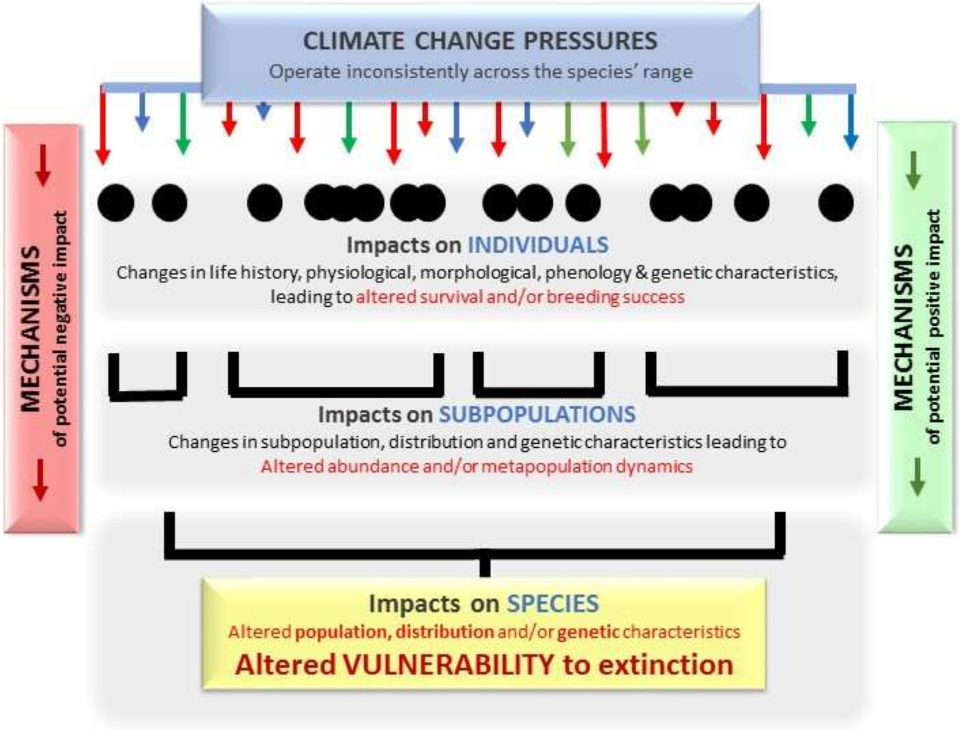

*Figure 4. Potential climate change impacts on species include the species-level population and range changes that underpin extinction risk. These changes are driven by changes at individual and subpopulation levels.*

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

| Impacts | Illustrative examples |
|---|---|
| **SPECIES LEVEL** | |
| **1. Population characteristics**<br>1.1. Changes in population size<br>1.2. Changes in proportion of mature individuals<br>1.3. Changes in sex ratio<br>1.4. Changes in magnitude and/or frequency of population fluctuations<br>1.5. Number of subpopulations | Gynther *et al.*, 2016 |
| **2. Range characteristics**<br>2.1. Changes in range size | Hickling *et al.*, 2006; Tingley *et al.*, 2009; Chen *et al.*, 2011; |

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

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

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

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| detrimental in the future. | |
| 4. Organisms experience change in **phenology** such that the timing of beneficial events or interactions are disrupted or enhanced. | Visser *et al*., 2006; Fryxell & Sinclair, 1988; Ludwig *et al*., 2006; Altwegg *et al*., 2012 |
| 5. Organisms experience changes in interactions with **non-climate change-driven threats** such that they are exacerbated (e.g. overharvesting, invasive species, land use changes) | Frederiksen *et al.*, 2004; Walther *et al.*, 2009; Schweiger *et al.*, 2010; Van Zuiden & Sharma, 2016; Kovach *et al.*, 2017 |

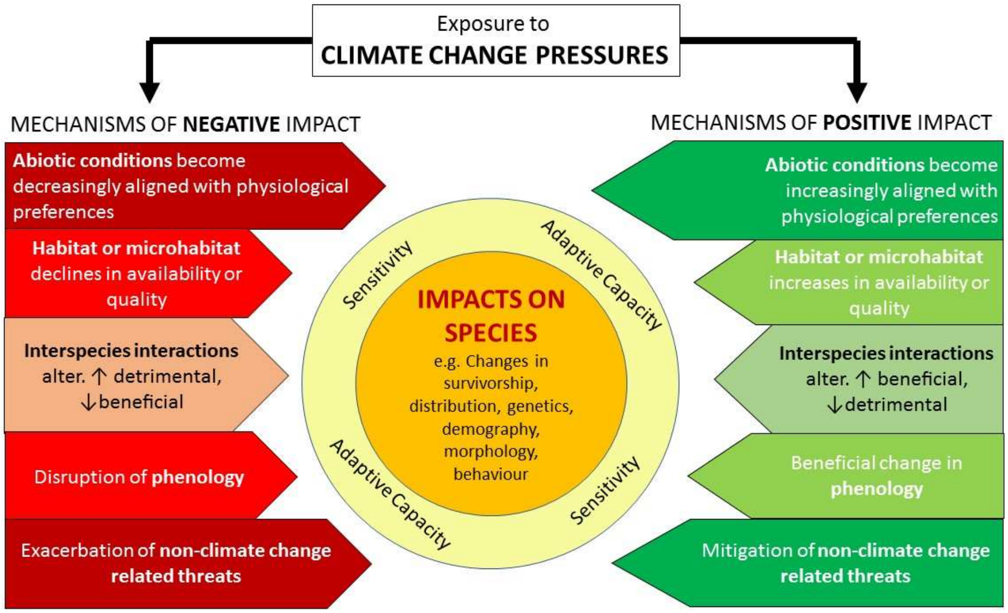

*Figure 5. Mechanisms describe the pathways through which climate change pressures may exert impacts on species. These impacts may have positive and/or negative impacts on the species and are mitigated or exacerbated by species' individual sensitivities and adaptive capacities.*

## Sensitivity

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

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

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.

## Adaptive Capacity

Adaptive capacity has been defined as 'the potential, capability, or ability of a species, ecosystem or human system to adjust to climate change, including changes in climate variability and extremes, so as to moderate potential negative outcomes, to take advantage of opportunities, or to respond to the consequences' (based upon IPCC WGII definitions, IPCC, 2007, 2014). The concept of adaptive capacity was developed with respect to human systems, and with its origins in organizational theory and sociology, emphasized system attributes such as governance, economic resources, technology, and levels of education (Engle, 2011). The concept has been applied in an ecological context to reflect those capacities of a system (whether a species or ecosystem) that enable it to adjust to or cope with changing conditions. In practice, the application of adaptive capacity to species and other natural resources has been challenging. In particular, many of the attributes that confer such adaptability overlap with features also associated with 'sensitivity' (e.g. habitat specialization, physiological tolerances, interspecific dependencies). At its root, the term 'adaptive' suggests modification or adjustment, and thus the concept of adaptive capacity can perhaps best be thought of as the ability of a species to accommodate a given stressor or change through some form of adjustment. The ability to adjust to changes is facilitated by high levels of phenotypic plasticity dispersal ability, or ‘evolvability’ (associated with its genetic diversity). These in turn can enable a species to adjust to new conditions by shifting locations, by modifying behaviours, physiology or life history factors, or by evolving new and more ‘adaptive’ traits (Table 4).

Adaptive capacity includes both intrinsic and extrinsic elements, and in that sense is context specific. Intrinsic factors include the dispersal, phenotypic and genetic attributes noted above. Extrinsic factors, however, may constrain or promote the expression of those adaptive capabilities. For example, even if a species has high dispersal capacity, if surrounding landscape conditions are inhospitable to the species or its propagules, there will be limited opportunities for dispersal-based coping. Indeed, the interplay between such intrinsic and extrinsic factors led Beever *et al*. (2016) to suggest an analogy for adaptive capacity based on classic ecological niche theory, as first proposed by Hutchinson (1957). In this conception, the *fundamental adaptive capacity* reflects a species’ intrinsic ability to accommodate climate change without significant genetic losses, large range contractions or extinction, or intensive management intervention. The *realized adaptive capacity*, in contrast, reflects how extrinsic factors constrain or limit expression of those intrinsic adaptive capacity factors. Under this framework, adaptation can be viewed as those actions or efforts capable of relaxing extrinsic constraints (particularly anthropocentric stressors) and shifting the realized adaptive capacity further towards the fundamental condition.

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

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

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

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

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

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

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

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

## CARRYING OUT CCVA OF SPECIES

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

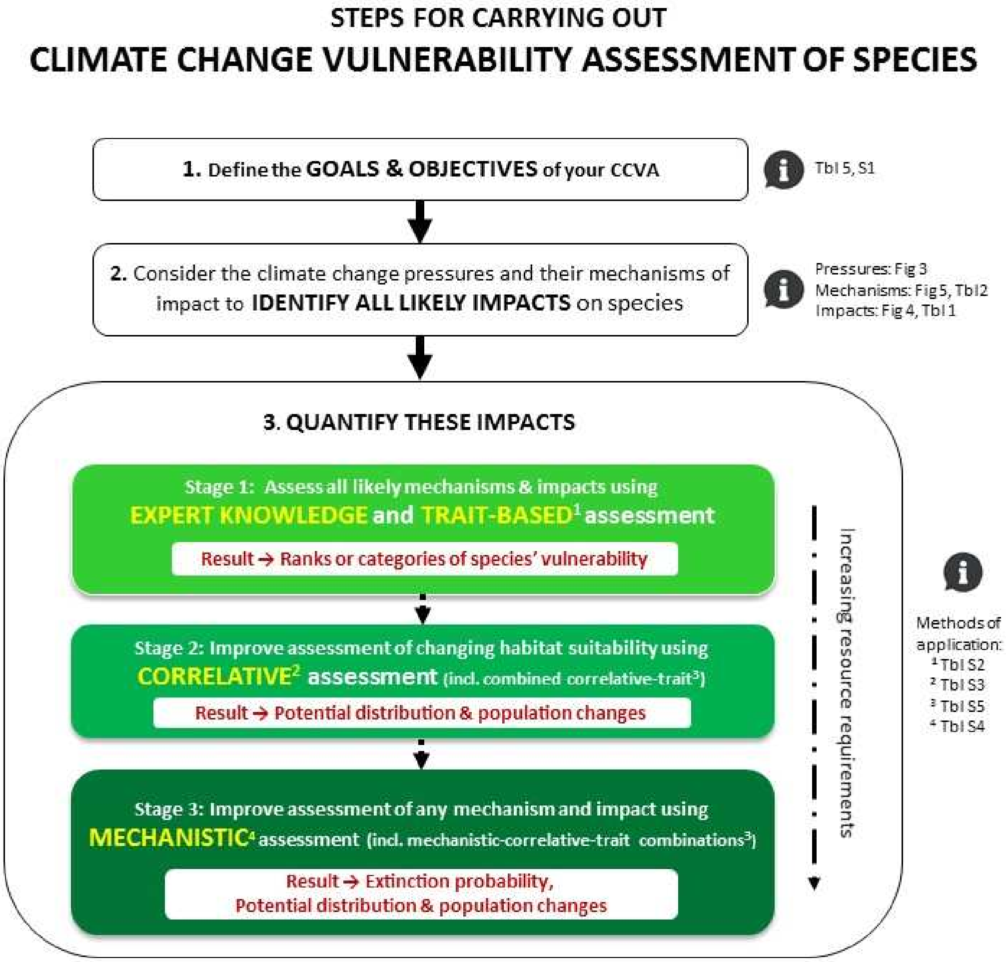

*Figure 6. The approaches used to carry out each of the three assessment types and the metrics or types of information of climate change vulnerability that they may produce.*

### Step 1: Define your goal and objectives

A well-defined *goal* explains why a CCVA is being undertaken, who the audience is and which decisions are intended to be influenced (Stein *et al*., 2012; Foden & Young, 2016). CCVAs can be carried out, for example: to determine the degree of vulnerability to climate change of one or more species in a region or across their entire ranges; to provide input into a specific adaptation planning process; to inform academic research (such as to generate input into a demographic model); or as an educational exercise to provide the basis for teaching about how climate change might influence species of interest. Identifying the audience, whether it be policymakers, land/resource managers, scientists or the public, will inform the level of complexity needed for the analyses and the strategy for communicating the results. If a CCVA aims to influence management practices, then understanding the planning and management context for the species to be assessed will allow the crafting of CCVA objectives and outputs to maximise their impact on those management processes, with correspondingly greater benefits for the conservation of the species.

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

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

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

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

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

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

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

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

**Step 3: Quantify the impacts**

In this step, the likely climate change mechanisms and their impacts identified in Step 2 are quantified according to three stages of increasing complexity, data and resource requirements, and applicability of resulting vulnerability metrics (Figure 6); each may help to inform the choice of focal mechanisms and impacts for subsequent stages. Assessors' choices of which stage(s) to complete typically include consideration of a) which deliver the vulnerability metrics needed to meet their CCVA objectives, and b) which they have sufficient resources (e.g. data, expertise, time) to apply. Where no alignment can be reached between these two considerations, assessors may consider revisiting objectives and/or mobilising additional resources. The three stages of complexity correspond approximately with predominant CCVA approaches, namely *trait-based*, *correlative* and *mechanistic approaches,* while the *combined approach* is applicable to stages two and three. We outline each approach, discussing its strengths and limitations, methods of application, examples of use and the vulnerability metrics it delivers. More detailed discussions can be found in Pacifici *et al.* (2015).

In all cases, we recommend beginning with an expert-based assessment. This involves examining the range of likely impact mechanisms in relatively non-technical and non-statistically intensive ways, with the aim of categorising and potentially prioritising mechanisms according to their likely impacts on focal species. At the most basic level, this involves considering species' exposure to climate change pressures and, using available knowledge of the species' sensitivity and adaptive capacity to estimate the likely relative or absolute magnitude of the impacts on the species. Red List assessments may provide valuable information for such assessments because they help to identify species with demographic and/or behavioural characteristics that increase their sensitivity; they also identify other pressures faced by species that may be exacerbated by climate change. Notwithstanding their limitations, expert-based assessments provide a valuable foundation for identifying factors and mechanisms to focus on in subsequent stages.

### *Trait-based approach*

This approach draws on the growing knowledge-base on associations between biological traits and climate change impacts (e.g. Cardillo *et al*., 2008; Murray *et al*., 2009; Thaxter *et al*., 2010; Angert *et al*., 2011; Chessman, 2013; Newbold *et al*., 2013; Pearson *et al*., 2014; Estrada *et al*., 2015), and makes use of a range of biological and life history information to score or rank species' probable sensitivity and adaptive capacity to climate change. These are often combined with assessments of exposure (e.g. Williams *et al*., 2008; Young *et al*., 2012; Foden *et al*., 2013b; Smith *et al*., 2016). While in the strictest sense, 'traits' refer to the characteristics of an individual (Violle *et al*., 2007), in the context of CCVA of species the term is generally used more loosely to refer to a broad range of species-level characteristics, examples of which are shown in Table 6 . Data relating to these traits may be qualitative, categorical or quantitative; categories must be ranked according to risk, whilst where trait data are quantitative, thresholds must be defined to determine risk categories. Trait-level scores or ranks are then combined qualitatively or semi-quantitatively to assign species into categories of vulnerability. We categorise methods for applying the trait-based approach according to the ways in which their scores are developed (i.e. Qualitative vs. Semi-Qualitative) and describe available tools, data requirements and examples (Supplementary Table 3). Trait-based approaches may include the outputs of correlative and mechanistic approaches (e.g. Küster *et al.*, 2011; Young *et al.*, 2012; Pompe *et al.*, 2014) or be included in other approaches (e.g. Garcia *et al.*, 2014a); we discuss these further under the 'Combined approach'.

Because the trait-based approach requires ecological knowledge without strong modelling or statistical expertise, and because it facilitates assessment of large numbers of species relatively rapidly (Pacifici *et al*., 2015; Foden & Young, 2016), it has been adopted by many conservation organizations. Limitations of the approach include the high degree of uncertainty about the links between species' traits and climate change impact, as well as gaps in the availability of species-level data for desired traits. Quantifying thresholds for high vs. low vulnerability for each trait is also challenging, resulting in thresholds that are often arbitrary and relative (Thomas *et al*., 2011; Foden *et al*., 2013; Pacifici *et al*., 2015). Approaches for combining trait scores, discussed in detail in Huntley *et al*. (2016), also remain challenging and typically produce categorical outputs. A study comparing observed population trends in British birds and butterflies with CCVA results showed poor predictive ability by trait-based assessments (Wheatley *et al*., 2017); further validation and method development are necessary. However, trait-based CCVAs remain valuable for exploring species' sensitivity and adaptive capacity to climate change, as well as for understanding the relative roles that potential impact mechanisms may have on the extent and nature of species' vulnerability to climate change.

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

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

*Correlative approach*

Perhaps better termed the 'Climate-matching approach', this includes 'niche-based', 'climate envelope' and 'species distribution modelling'. Correlative assessment depends upon fitting models that describe the correlation between each focal species' distribution, usually in the recent past (i.e. the late twentieth century), and the contemporary climate. The fitted model aims to reflect the species' realised niche (Hutchinson, 1957) during the period to which the distribution and climate data relate and can be used to infer its climate requirements or ecological tolerances. Correlative assessments can be used to identify those geographical areas where climate is likely to be suitable for the species under any projection of potential future climate (Pearson & Dawson, 2003; Beale *et al*., 2008), and hence to estimate its potential distribution under those climate conditions. A species' climate change vulnerability is inferred from differences between its recent distribution and its predicted potential future distribution in terms of extent, location and sometimes degree of fragmentation (e.g. Garcia *et al*., 2014a), and also their degree of overlap (Huntley *et al*., 2007). Correlative approaches have been used to predict species' potential distribution changes at various spatial scales (Pacifici *et al*., 2015), and have been widely applied to assess climate change vulnerability of plants (Midgley *et al*., 2002; Thuiller *et al*., 2005; Fitzpatrick *et al*., 2008), invertebrates (Harrison *et al*., 2006; Settele *et al*., 2008; Heikkinen *et al*., 2010; Sánchez-Fernández *et al*., 2011) and vertebrates, including birds (Gregory *et al*., 2009; Hole *et al*., 2011; Garcia *et al*., 2012), mammals (Hughes *et al*., 2012; Songer *et al*., 2012; Visconti *et al*., 2015), amphibians (Lawler *et al*., 2009; Carvalho *et al*., 2011) and fishes (Jeschke & Strayer, 2008; Yu *et al*., 2013). We categorise methods for applying the correlative approach as climate envelope, regression-based, machine learning and Bayesian, and describe available tools, data requirements and examples of their application (Supplementary Table 4).

Correlative assessments are very widely used, probably because methods of application are relatively rapid and cost-effective, occurrence data required are easily available for a large number of taxa, and due to their applicability for spatial conservation planning (e.g. Hannah *et al*., 2002; Araujo *et al*., 2004; Phillips *et al*., 2008; Araújo *et al*., 2011). Choice of modelling technique is one of the major sources of uncertainty in correlative models (Diniz-Filho *et al*., 2009; Garcia *et al*., 2012) but valuable guidance on using and understanding correlative models is available, including from (Pearson, 2007; Franklin, 2009; Peterson *et al*., 2011; Anderson, 2012, 2013). Shortcomings of correlative CCVAs have been widely discussed (e.g. Pearson & Dawson, (2003b), Hijmans & Graham (2006), Hannah *et al*., (2007), Araújo & Peterson (2012) and Pacifici *et al*., (2015)); their assumption that species' distributions are in equilibrium with the prevailing climate can prove problematic in cases where a species' contemporary distribution reflects the outcome of recent or historical pressures (e.g. habitat loss, persecution) or natural dispersal barriers that have excluded the species from areas of suitable climate (Guisan & Thuiller, 2005). Other challenges include poor performance for species with few records (see section below on 'Species that pose particular CCVA challenges'), failure to account for local adaptation, and difficulty in projecting suitability for novel climatic conditions (i.e. outside the climatic range of the training data).

When validated using species' observed responses to recent climate changes, however, correlative CCVAs have been shown to perform well in predicting species' population increases/decreases in many cases (Green *et al*., 2008; Gregory *et al*., 2009; Stephens *et al*., 2016) and to have a fair ability to predict distribution changes (e.g. Chen *et al*., 2011; Dobrowski *et al*., 2011; Morelli *et al*., 2012; Smith, 2013). The range of potential impact mechanisms may be increased, for example, by incorporating variables such as inter-species interactions (e.g. Schweiger *et al*., 2008, 2012), the availability of nesting sites (e.g. Heikkinen *et al.*, 2007) and habitat shifts (e.g. Thuiller *et al.*, 2006a) along with climate variables in models. Further advances are being made by combining correlative and trait-based approaches, including by incorporating estimates of dispersal ability (e.g. Warren *et al.*, 2013) and sensitivity and adaptive capacity (e.g. Garcia *et al.*, 2014a) into projections of species' range shifts (see 'Combined approach' and 'Improving CCVA methodology' below).

### *Inferring distribution changes from model projections*

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

### *Inferring population changes from distribution changes*

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

*Mechanistic approach*

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

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

*Combined approach*

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

Garcia *et al.*, 2014a) to improve range shift predictions (i.e. a correlative-trait approach). Correlative and mechanistic approaches may be used in combination to enable inclusion of a range of potentially important variables for predicting the suitability of potential future range, including metapopulation dynamics and environmental processes such as sea level rise, fires and stochasticity (e.g. Keith *et al.*, 2008; Anderson *et al.*, 2009; Midgley *et al.*, 2010; Fordham *et al.*, 2012), as well as inter-species interactions (e.g. Harris *et al.*, 2012; Fordham *et al.*, 2013) (i.e. a correlative-mechanistic approach). Finally, all three approaches may be combined in Criteria-based assessments in which species are classified into categories of risk based on the information from correlative and/or mechanistic assessments, species trait data and observed species changes (e.g. Thomas *et al.*, 2011) (i.e. a correlative-mechanistic-trait Approach). We provide further details of combined approaches, including data requirements, available tools and examples of their application (Supplementary Table 6), and discuss their potential for advancing CCVA of species under 'Future directions'.

## SELECTING AND USING CCVA INPUT DATA

A growing body of data and resources for CCVA of species is now available online but selecting and using these appropriately can be challenging (Wade *et al*., 2017). We discuss these below and provide summaries of CCVA resources in Supplementary Tables 7 and 8; a synthesis of the input data requirements for trait-based, correlative and mechanistic CCVA approaches is also provided (Supplementary Table 9). An important first consideration in setting the parameters of the assessment is defining the spatial extent and resolution of the CCVA. The *spatial extent* of a CCVA is the total area under consideration; this may be specified by the CCVA objective and/or encompass the distribution range of focal species. Two important considerations help to avoid over-estimating vulnerability when predicting areas of suitable climate in the future. Firstly, for species-focused CCVA objectives, including the full distribution range is important for estimating the species' full niche breadths. Secondly, it is important to include sufficient area around the current range such that the spatial extent includes all areas that could feasibly become suitable for the species in the future time frames considered. Considering an excessively large area, however, will inflate model accuracy and pick up broad-scale rather than finer-scale differences in suitability (e.g. Anderson & Raza, 2010).

*Spatial resolution* or grain is relevant when CCVA is to be carried out using a modelling approach that requires gridded data and refers to the grid cells' area or linear dimensions. Ideally, the spatial grid size should be ecologically relevant for the study species (i.e. reflecting relevant ecological processes) and capture the way individuals perceive the environment (Potter *et al*., 2013). In practice the grid size used in most studies is orders of magnitude larger and is often be determined by the resolution of data available, since the essential dataset with the coarsest resolution generally determines the limit to which grain size can be reduced. For example, whilst elevation data may be available on a 50m grid (i.e. 50m x 50m), if species' distribution data are recorded for a 1km grid, the latter is the finest grain size possible for most analyses (Foden & Young, 2016). Finer resolutions may be necessary to represent areas of higher spatial heterogeneity (e.g. topographically complex or with varying land-surface properties), but the associated increase in computational demands as grain size reduces typically poses a practical limit. At resolutions >20km, species' abundance and distributions can generally be explained by bioclimatic variables alone (Luoto *et al.*, 2007), but at finer scales variables related to habitat suitability, land use and management become important, and below 1 km microclimate becomes dominant. In the latter case, microclimate influences should be explored taking into account factors such as slope, aspect, vegetation and shading by adjacent areas at higher elevation (see e.g. Bennie *et al*., 2008, 2013; Gillingham *et al.*, 2012; Hodgson *et al.*, 2015). At almost all grain sizes relevant to CCVAs important issues that arise with respect to downscaling climate model outputs should be considered (Baker *et al*., 2017).

**Species data**

*Distributions*

For methods that rely on occurrence or locality records to characterise species' bioclimatic tolerances (i.e. correlative modelling approaches), using data of good quality is particularly important. Ideal sources include surveys or atlases, and well-validated specimen and citizen science records. Data from large distribution databases (Supplementary Table 7) provide a convenient source of data but must be carefully reviewed for accuracy. Where available, data on species' abundances (or based on abundance proxies such as reporting rate) are especially valuable. Expert-developed range polygons may be used when they are based on first-hand knowledge of current species occurrence or where gridded data or point records are unavailable, but they are likely to have a higher incidence of false presences (commission errors) especially if patchiness in the species' distribution within polygons is not accounted for.

False presences also arise from species misidentification or taxonomic uncertainty, incorrect locality recording or data entry error, and can lead to overestimation of species' environmental niches. The most common cause of uncertainty, however, is false absences (omission errors). These typically arise from spatial differences in sampling effort (e.g. low sampling effort away from roads, in inaccessible areas, or in countries with limited resources to survey biodiversity), differences in detectability (e.g. fewer records of cryptic species) or in level of interest/charisma (e.g. disproportionate number of records for charismatic species). Some datasets provide data from which detection probability can be estimated (e.g. Southern African Bird Atlas Project (Harrison *et al.*, 1997) Breeding Bird Surveys ( Massimino *et al.*, 2017) or on areas where the species was sought and not found (e.g. European Bird Census Council Atlas (Hagemeijer & Blair, 1997). For correlative models, Guillera-Arroita *et al*. (2015) provide guidance on how the type of distribution data (and associated sampling bias) determines the quantity that is estimated by the models. Various approaches have been proposed to address spatial biases in species' presence data. Phillips *et al.*, (2009) developed models that use all records of presence for members of a group of species to generate a background sample of pseudo-absences for the focal species that have the same spatial bias as the collective presence records. Other approaches include Bayesian approaches (Manceur & Kühn, 2014; Rocchini *et al*., 2017), subsampling in geographic space (Aiello-Lammens *et al*., 2015) or in environmental space (Varela *et al.*, 2014), and weighting presences by the inverse of their density (Stolar & Nielsen, 2015).

*Trait and life history information*

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

## Climate data

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

*Bioclimatic variables*

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

Autecological studies identifying precise bioclimatic variables that affect a particular species' performance or survival, and their mechanisms of action, are rare (e.g. Pigott & Huntley, 1981). However, general biological knowledge accumulated for a variety of taxonomic groups and climate regions, assessments of bioclimatic variable performance (e.g. Barbet-Massin & Jetz, 2014) and previous published models provide a basis for an informed choice of bioclimatic variables for most species. Mean annual temperature or precipitation are unlikely ever to be mechanistically important (Bateman *et al*., 2012; Huntley, 2012; Platts *et al*., 2013) but coldest and/or warmest month means or annual extremes and annual thermal sums above or below relevant thresholds, for example, have well-understood mechanistic roles for a wide range of taxonomic groups. For higher plants, the balance between precipitation and evaporation is mechanistically relevant, while members of other taxonomic groups may be greatly influenced by the distribution of precipitation through the year. Other taxon-specific measures relating to particular periods of high sensitivity to weather conditions, such as the breeding season (Pearce-Higgins *et al*., 2015a) may also be considered.

Regionally, for tropical species, relevant bioclimatic variables are likely to include a combination of coldest and warmest month mean temperatures, annual ratio of actual to potential evapotranspiration, the intensity of the dry/wet season, and measures of rainfall bimodality (i.e., two rainy seasons in a year). For temperate species, the best default bioclimatic variables are likely to include the coldest month mean temperature, annual thermal sum above 5°C, and the annual ratio of actual to potential evapotranspiration. For some cool temperate species that have a 'chilling' requirement, a measure of the length of the period with temperatures below a threshold (e.g. 0°C), or the (negative) annual thermal sum below 0°C can be an important additional variable, as well as snow water equivalent (SWE).

*General Circulation Models (GCMs).* GCMs are computationally intensive mathematical models of atmosphere and ocean processes that are used to generate weather forecasts and climate change projections. GCM outputs differ due to dissimilarities in the ways that models simplify and simulate *extremely* complex systems, as well as due to knowledge-gaps in climate science. No GCM perfectly reproduces all of the features of the global climate system, so use several models to understand the uncertainties in projections is essential. Fordham *et al*. (2011, 2012) offers some tools for model selection, ensemble building based on model skill, and downscaling. Model inclusion by the IPCC in a recent report (IPCC, 2013) conveys legitimacy, and those selected should reflect the range of uncertainty amongst models by including those that are relatively 'warm', 'cool', 'wet', and 'dry', as well as those whose mean temperature and precipitation projections are near the mean of all models. Models that perform 'best' in the geographical region of interest should be favoured (Baker *et al*., 2015). Where possible, use of observed climate data to assess model performance under past conditions in CCVA focal areas is also valuable. The IPCC's Data Distribution Centre is a portal for a broad range of GCM outputs.

Projections from the individual models selected, collectively referred to as the model 'ensemble', may be averaged to produce a single projection, with the degree of agreement between projections represented by a measure of 'spread' such as the standard deviation or coefficient of variation (for details and caveats of model averaging, see Dormann *et al.* (2018)). While this is often carried out in other contexts, for CCVA this is inadvisable because it provides little insight into the uncertainty of CCVA outputs. Conducting individual assessments using projections from several (at least three) individual models is preferable to a single assessment applied to one model ensemble. Additionally, since different models may generate qualitatively different circulation patterns, averaging them could also result in an ensemble mean projection that is mechanistically unrealistic or physically impossible, or that disguises year-to-year variations that may be important drivers of vulnerability.

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

### *Greenhouse Gas Trajectories and Emissions Scenarios*

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

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

### Ecological data

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

### Data on human response pressures

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

## SPECIES THAT POSE PARTICULAR CCVA CHALLENGES

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

Efforts to fill data gaps and use conventional CCVA methods can rely on inferences from data for related species (Foden *et al*., 2013), expert opinion (Murray *et al*., 2009; Martin *et al*., 2015), data imputation techniques, or a combination of literature and targeted fieldwork (Williams *et al*., 2009). Conventional CCVA methods can be modified to accommodate incomplete data. Correlative modelling of poorly-known and small-range species can rely on simplified correlative techniques (Hof *et al*., 2011; Platts *et al*., 2014), more complex techniques with adjusted parameters (Hof *et al*., 2011), methods that account for potential biases in sampling effort (Beale *et al*., 2014), or consensus building around several models based on a small number of predictors (Lomba *et al*., 2010). For declined-range species, correlative models could overestimate climate change vulnerability if, for example, warmer parts of the range have been lost for non-climatic reasons (e.g. deforestation at low elevations); therefore, the extant range should be augmented with information on the historic range whenever possible. Another modification to conventional CCVA methods is to redefine taxonomic focus of the models, selecting either a resource used by the focal species that has sufficient data (Delean *et al.*, 2013), or a species assemblage that includes the focal species. Assemblages can be defined with reference to community types (Ferrier & Guisan, 2006), biomes (Midgley *et al.*, 2003), or shared traits (Golicher *et al.*, 2008; Vale & Brito, 2015) that are thought to mediate species' responses to climate change. Caution is needed, however, in the use of such approaches given the evidence from the Quaternary record of the individualistic responses of species to past climate changes (e.g. Huntley, 1991; Graham *et al.*, 1996) and the resulting impermanence of species assemblages (e.g. Graham & Grimm, 1990; Huntley, 1996).

Alternative approaches make use of available data to draw inferences about species' vulnerability to climate change (Table 7). When historical data on population and climate variability are available, temporal analysis can be used to identify long-term trends in potential climate drivers of population change and infer future population changes under projected climates (Pearce-Higgins *et al.*, 2017). When the information available is restricted to climate data, assessments can be based solely on the exposure of geographical areas to climate changes. Analysis of multiple dimensions of climate change, such as velocities of temperature change or the disappearance of specific climate conditions, and associated threats and opportunities for species (Garcia *et al.*, 2014b) can provide indications of the likely vulnerability of species present in such areas (Ohlemuller *et al.*, 2008; Garcia *et al.*, 2014a).

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

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

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

## RED LIST ASSESSMENTS AND CCVA

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

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

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

## FUTURE DIRECTIONS

### CCVA validation

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

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

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

Combined CCVAs incorporate different (depending on the specific method) types of information about the attributes of species, environments they occupy, and their empirical population and distribution trends, as well as ctorrelative model-based projections. There has been relatively little validation of trait-based CCVAs, although it is possible to do so by comparing results of the assessment for a species against observed changes in that species' distribution or abundance under climate change (where available). One recent study (Wheatley *et al*., 2017) using this approach found that trait-only CCVAs did not predict changes in status through time successfully whereas methods that included population and/or distribution trends (incorporating correlative projections) as well as some trait information (e.g. habitat and dispersal constraints) could predict changes in status. This validation was limited to one geographic region over a relatively short time period, so further work is required to broaden the scope of CCVA validation and establish which methods work best under different circumstances.

### Improving biodiversity data

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

### Advancing CCVA methodology

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

*Better consideration of climate extremes and variability*

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

**Incorporating molecular information**

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

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

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

## Incorporating adaptive genetic change and phenotypic plasticity

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

## Approaches to uncertainty

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

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

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

## FURTHER READING

### Resources for climate change adaptation and vulnerability assessment

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

## FIGURES AND TABLES

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

**Sidebar title:**

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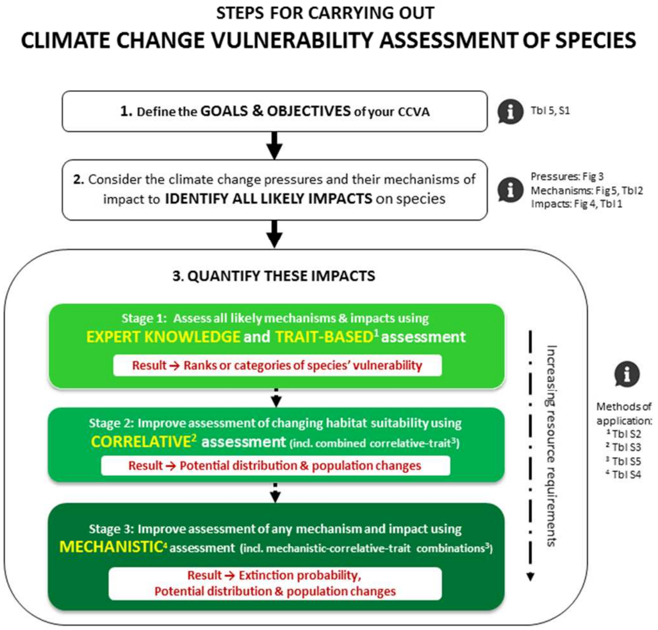

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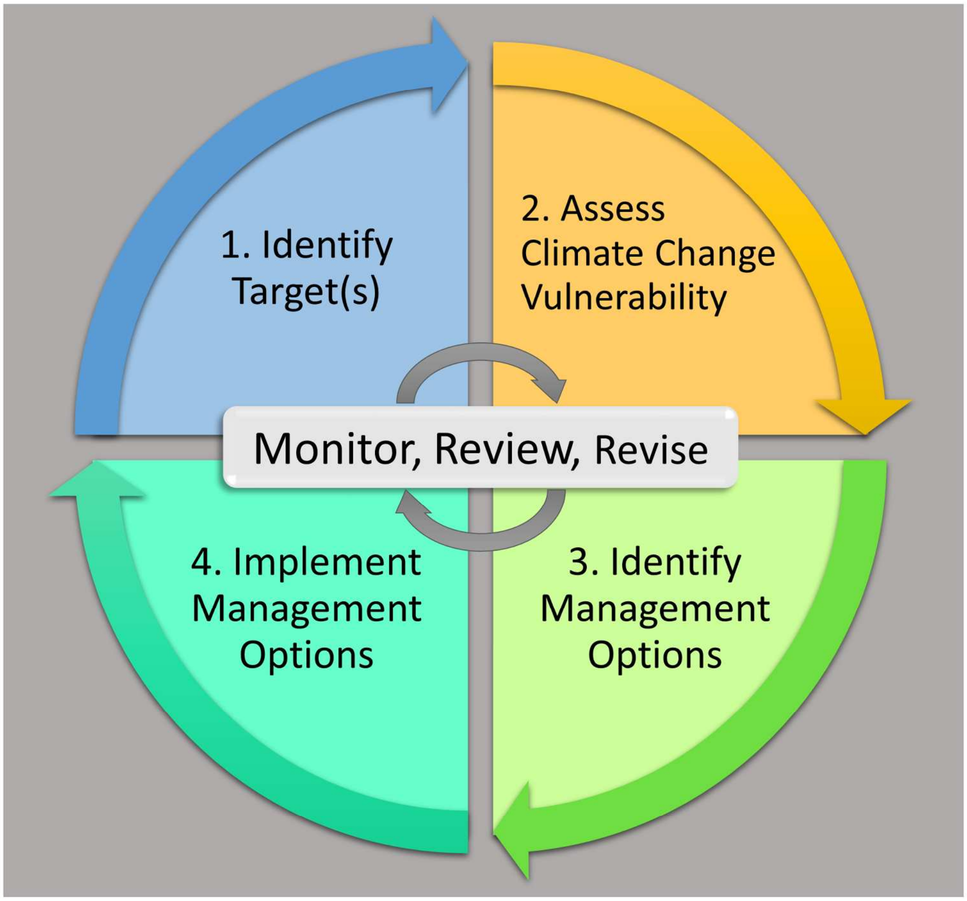

Figure 1: Steps for developing climate change adaptation strategies (Adapted from Glick et al. (2011))

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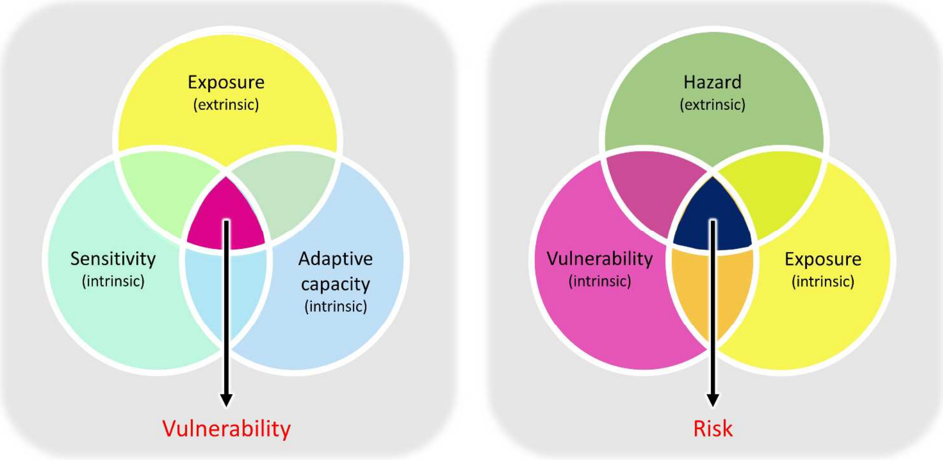

Figure 2a. According to the IPCC Fourth Assessment (2007) and common usage in the field of CCVA of species, vulnerability to climate change results from the interaction of exposure and sensitivity with adaptive capacity (adapted from IPCC, 2007).

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

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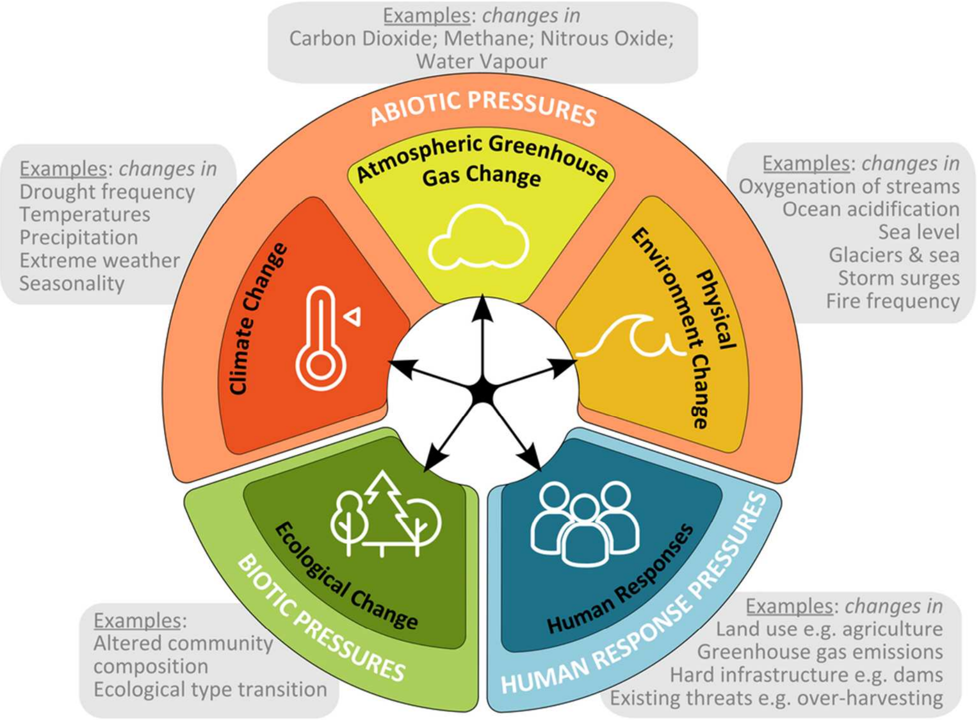

Figure 3. Climate change related pressures on species, showing those originating from abiotic, biotic and human response causes.

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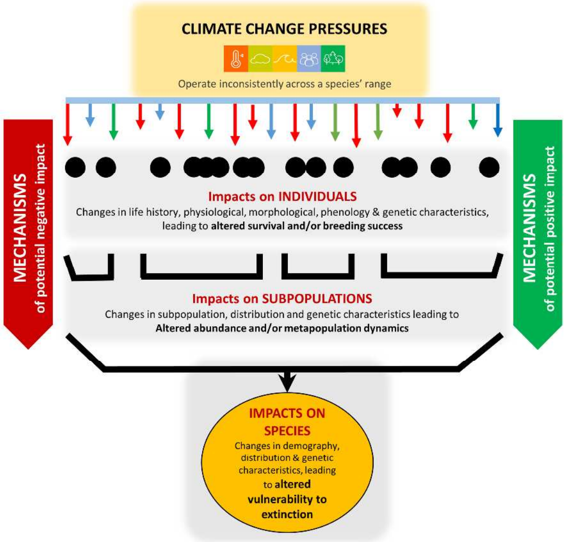

Figure 4. Potential climate change impacts on species include the species-level population and range changes that underpin extinction risk. These changes are driven by changes at individual and subpopulation levels.

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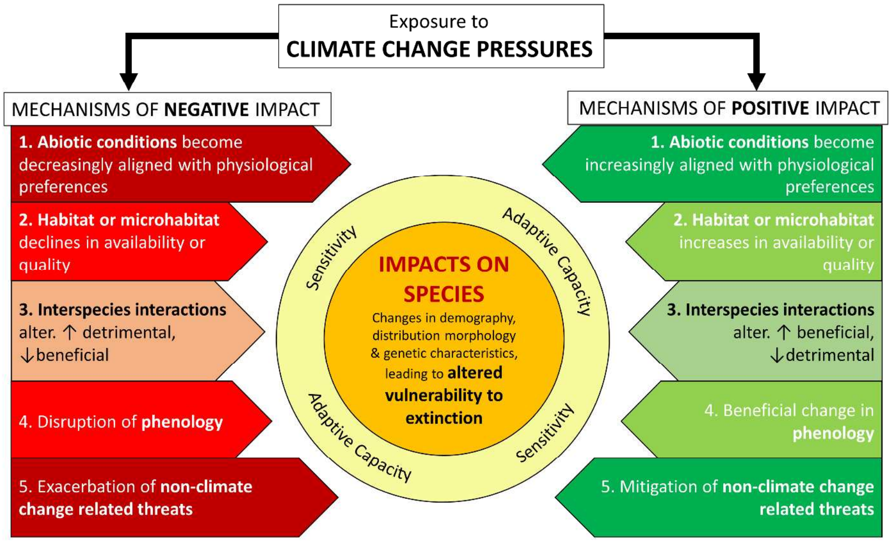

Figure 5. Mechanisms describe the pathways through which climate change pressures may exert impacts on species. These impacts may have positive and/or negative impacts on the species and are mitigated or exacerbated by species' individual sensitivities and adaptive capacities.

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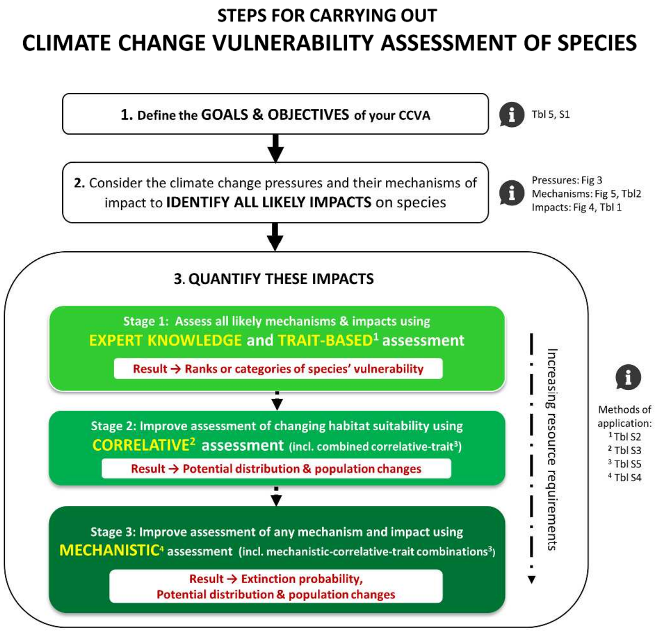

Figure 6. The approaches used to carry out each of the three assessment types and the metrics or types of information of climate change vulnerability that they may produce.

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