



Integrating climate change vulnerability assessments from species distribution models and trait-based approaches



S.G. Willis^{a,*}, W. Foden^b, D.J. Baker^a, E. Belle^c, N.D. Burgess^{c,d}, J.A. Carr^e, N. Doswald^c, R.A. Garcia^{f,g,h}, A. Hartleyⁱ, C. Hof^j, T. Newbold^c, C. Rahbek^h, R.J. Smith^k, P. Visconti^l, B.E. Young^m, S.H.M. Butchartⁿ

^a School of Biological & Biomedical Sciences, Durham University, Mountjoy Site, Durham DH1 3LE, UK

^b Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg 2050, South Africa

^c UNEP-WCMC, 219c Huntingdon Road, Cambridge CB3 0DL, UK

^d Conservation Science Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

^e IUCN Global Species Programme, 219c Huntingdon Road, Cambridge CB3 0DL, UK

^f Department of Biogeography and Global Change, National Museum of Natural Sciences, CSIC, Calle José Gutiérrez Abascal 2, 28006 Madrid, Spain

^g CIBIO-InBIO, Universidade de Évora, Casa Cordovil 2º Andar, Rua Dr. Joaquim Henrique da Fonseca, 7000-890, Évora, Portugal

^h Centre for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, DK-2100 Copenhagen, Denmark

ⁱ Met Office Hadley Centre, FitzRoy Road, Exeter, Devon EX1 3PB, UK

^j Senckenberg Biodiversity and Climate Research Centre (BiK-F), Senckenberganlage 25, 60325 Frankfurt, Germany

^k Durrell Institute of Conservation and Ecology, School of Anthropology and Conservation, University of Kent, Canterbury, Kent CT2 7NR, UK

^l Microsoft Research Computational Science Laboratory, 21 Station Road, CB1 2FB Cambridge, UK

^m NatureServe, Apdo. 358-1260, Plaza Colonial, San Jose, Costa Rica

ⁿ BirdLife International, Wellbrook Court, Girton, Cambridge CB3 0NA, UK

ARTICLE INFO

Article history:

Received 1 May 2014

Received in revised form 24 April 2015

Accepted 1 May 2015

Available online 19 June 2015

Keywords:

Species distribution modelling

Species climate vulnerability traits

Model integration

Conservation planning for climate change

ABSTRACT

To accommodate climate-driven changes in biological communities, conservation plans are increasingly making use of models to predict species' responses to climate change. To date, species distribution models have been the most commonly used approach for assessing species' vulnerability to climate change. Biological trait-based approaches, which have emerged recently, and which include consideration of species' sensitivity and adaptive capacity, provide alternative and potentially conflicting vulnerability assessments and present conservation practitioners and planners with difficult choices. Here we discuss the differing objectives and strengths of the approaches, and provide guidance to conservation practitioners for their application. We outline an integrative methodological framework for assessing climate change impacts on species that uses both traditional species distribution modelling approaches and biological trait-based assessments. We show how these models can be used conceptually as inputs to guide conservation monitoring and planning.

Crown Copyright © 2015 Published by Elsevier Ltd. All rights reserved.

1. Introduction

Biodiversity loss is occurring across much of the world (Butchart et al., 2010; Secretariat of the CBD, 2010; WWF, 2012) and anthropogenic climate change has been identified as one of the main drivers of these trends (Parmesan and Yohe, 2003). This threat is predicted to become more severe over the next century owing to accelerating global warming, and changes in precipitation patterns and timings, as well as alterations in climatic extremes (IPCC, 2007). Various predictions have been made of the impacts of climate change on the world's habitats and species, generally

indicating that more species will become threatened with extinction, and that their distributions will move substantially, often shrinking (Sala et al., 2000; Midgley et al., 2002; Thomas et al., 2004; Bagchi et al., 2013). Climate change is not only additional to other direct threats to biodiversity, such as land-use change, over-hunting, and invasive species, but can also act synergistically with these threats (e.g. Benning et al., 2002; Hof et al., 2011). There is, therefore, an urgent need to assess the potential consequences of future climate change on species, and to initiate adaptive management planning that helps shape current and future conservation decisions. The need to produce adaptive management plans has stimulated considerable research in recent years, resulting in various approaches to assessing climate change-driven risks

* Corresponding author. Tel.: +44 (0)191 3341379.

E-mail address: s.g.willis@durham.ac.uk (S.G. Willis).

(Game et al., 2011; Hole et al., 2011; Gardali et al., 2012; Bagchi et al., 2013; Foden et al., 2013; Garcia et al., 2014).

To date, the majority of climate change vulnerability assessments have used Species Distribution Models (SDMs), which correlate data on species' contemporary distributions with observations of recent climates and then apply these correlations to climate projections to predict the location(s) of suitable climatic conditions for a species in the future (e.g. Beaumont and Hughes, 2002; Harrison et al., 2006; Phillips et al., 2006; Huntley et al., 2008; Jensen et al., 2008). Consequently, in predicting species responses to projected future climate change, SDMs use future exposure of a species to climate change (i.e. the extent to which the species' physical environment will change) to climate change as an input parameter and assess the sensitivity of the species (the potential for the species to persist, *in situ* or elsewhere) to that change. However, such SDMs take no account of the potential capacities of species to adapt to such changes by dispersal, behavioural change or evolutionary adaptation. For example, a species might have ample climatically-suitable habitat in the future, but its inherent dispersal limitations may make reaching this habitat unlikely. The shortcomings of using basic SDM approaches to simulate future species changes are well recognised (see Seo et al., 2009; Wiens et al., 2009; Sinclair et al., 2010), and include their lack of consideration of biological information about the likelihood of species realising distribution changes projected by SDMs (Pearson and Dawson, 2003). This shortcoming has led to the development of next-generation, dynamic (or process-based) SDMs that include relevant biological traits such as dispersal ability, habitat requirements and other key parameters to assess the likelihood of population changes being realised over space and time (Kearney and Porter, 2009; Conlisk et al., 2013). However, to parameterise such models requires quantitative data for a species or system; something that is lacking for many species. An alternative approach, which we term 'Trait-based Vulnerability Assessment' (TVA) considers the vulnerability of species to potential climate change based on the best available current knowledge of the species' ecology and life history. Unlike process-based models, TVAs use composite indices (as opposed to modelling) to characterise the vulnerability of species to climate change.

TVA approaches identify, for a species, the traits that are known or presumed to render it vulnerable to climate change impacts. This often entails consideration of three aspects of vulnerability: exposure to climate change, sensitivity to changes in climate, and capacity to adapt to such changes, with the latter two aspects benefiting from the consideration of traits. Species that combine high exposure, a high degree of sensitivity, and low capacity to adapt will be most vulnerable to climate change. These methods provide a relatively rapid approach to score species according to their likely vulnerability to future climate change (Rowland et al., 2011). Several variants on the TVA approach have recently been developed, and are being applied to increasing numbers of taxa (Williams et al., 2008; Chin et al., 2010; Dawson et al., 2011; Graham et al., 2011; Thomas et al., 2011; Young et al., 2011; Foden et al., 2013).

To date, however, there have been few explicit comparisons of SDMs and TVAs in terms of their objectives, the conceptual frameworks underpinning them (Rowland et al., 2011; Pacifici et al., 2015), and the results they produce (Garcia et al., 2014). Furthermore, little attempt has been made to demonstrate how their outputs can be applied at scales relevant for conservation decision making (national and smaller). We seek to address remaining gaps of these two approaches by considering how elements of each could be used to strengthen the other, and propose how they can be integrated to provide improved climate change vulnerability assessments. Our resultant framework also indicates how both approaches can feed into adaptive management planning

and spatial conservation prioritisation at scales where conservation decisions are made (Margules and Pressey, 2000; Moilanen et al., 2009; Ladle et al., 2011). We also outline some of the challenges in using the results of climate change vulnerability assessments within the framework of systematic conservation planning.

2. Species Distribution Models (SDMs)

SDMs, in their most basic form, correlate data on the distribution of a taxon (typically a species) with data on contemporary climates (relating to the same time period from which the distribution data were derived) to establish a relationship between climate and species occurrence. Resultant models (or more commonly suites of models) are then applied to future climate change projections to produce forecasts of species' potential future ranges. Such SDMs have been applied to species at scales ranging from global (Thomas et al., 2004) and continental (Garcia et al., 2012) to regional (Thuiller et al., 2005), and have been used to assess projected turnover of species in key sites or protected areas (Hole et al., 2009, 2011; Araújo et al., 2011; Bagchi et al., 2013). Such models are most often used to indicate climate change vulnerability by comparing the projected change in range size and location between the present and a future period (often under various scenarios of dispersal), or even the change in coverage by key sites or protected areas under future climate change (Coetzee et al., 2009; Bagchi et al., 2013).

However, there are a myriad of biotic and abiotic factors that limit the use of such projections for assessing species' climate change vulnerability; a consequence of the fact that such models aim principally to assess geographical shifts in climate suitability rather than species vulnerability *per se*. Such correlative models generally fail to reflect differences between species in terms of their biology (e.g. dispersal ability, tolerance of habitat degradation, demography and the way that species interact with one another), to incorporate population dynamics and information on current and projected land cover, or to account for the discrepancy between climatic preferences as inferred from species' realised geographical distributions and their fundamental climatic niches as determined by their physiology (e.g. Araújo et al., 2013; Khaliq et al., 2014). In addition, they often cannot be used for species with small geographic distributions or for which only few records are available (Williams et al., 2009), despite such species often being those of greatest conservation concern. Nonetheless, SDMs can provide useful preliminary indications of the potential spatial and temporal patterns of change in species abundance, distribution and community composition (Elith et al., 2006; Gregory et al., 2009).

3. Trait-based Vulnerability Assessments (TVAs)

TVAs aim to combine indices or scores for exposure to climate change and species-specific combinations of biological characteristics that may increase or decrease the effects of climate changes on a species, in order to gain some overall measure of vulnerability (Williams et al., 2008; Young et al., 2011; Gardali et al., 2012; Foden et al., 2013). They quantify exposure in a variety of ways, though these are typically simple, uniformly applied measures of change in climatic variables that are presumed or demonstrated to be relevant. These assessments consider intrinsic sensitivity and adaptive capacity but sometimes also add extrinsic factors that might influence a species' capacity to adapt (e.g. prevention of dispersal due to species-specific habitat barriers). In general, TVAs assume that vulnerability to climate change is a product of three components. Like SDMs they consider exposure and sensitivity, although sensitivity assessments in TVAs usually consider factors

additional to climate that could affect persistence. Assessment of sensitivity and adaptive capacity, considered together as ‘sensitivity’ by some approaches (e.g. Garnett et al., 2013), generally involves identifying the generic life history (e.g. reproductive output), ecological (e.g. microhabitat or interspecific dependencies) and genetic (e.g. known historic bottlenecks) characteristics that could render species vulnerable to climate change (see Table 1 for examples). Species are then scored according to these traits using the best available information (published, unpublished or expert knowledge). Finally, sensitivity, adaptive capacity and exposure scores may be weighted and are combined into an overall score or measure of climate change vulnerability for each species. A major area of uncertainty in TVAs is how to combine scores in a manner that reflects true vulnerability, as scores are often not on comparable scales and, as a result, may be standardised before being combined, which may mask true vulnerability. Different TVA methods adopt different approaches, for combining components of vulnerability including expert-based weighting (e.g. Graham et al., 2011), weighting by score confidence (e.g. Thomas et al., 2011) and logic frameworks (e.g. Foden et al., 2013). Validation of assessments using observed changes in species distributions and abundances remains an urgent priority for TVA approaches. Recent work by Pearson et al. (2014) provides a quantification of how traits may relate to extinction risk. Such work seeks to pave the way for robust approaches to combine the various components of TVAs into predictive models. Examples of TVA approaches, including the vulnerability dimensions and traits considered, are given in Table 1.

Because biological traits generally change little over decadal time-scales, the measures of adaptive capacity and sensitivity gathered during the TVA process can provide insights into species’ vulnerability that are not subject to the uncertainties of future climate change projections for this century (Foden et al., 2013). However, trait data are not always readily available for species, and consequently vulnerability scores are often heavily reliant upon expert opinion, which itself is sometimes limited. Also, because the degree of climate change vulnerability associated with any particular trait is seldom known or empirically quantified, TVAs face large challenges in setting thresholds for each trait to

categorise the degree of climate change vulnerability. Many approaches circumvent this constraint by using ordinal scoring and producing *relative* rather than *absolute* measures of climate change vulnerability. However, this can provide challenges for interpreting and applying results.

TVAs have generally been designed to be practical, accessible and easily applied, and most have therefore avoided the traditionally complex and technically demanding processes associated with SDMs. The often simplistic assessment of climate change exposure means, however, that spatially explicit information such as the relationship between current and projected distribution ranges, and the threats that are likely to operate in the potential future distribution ranges, are not considered. While maps of the numbers and proportions of species vulnerable to climate change can provide insight into areas of highest vulnerability to species loss, most do not predict potential species gains, and are hence unhelpful in projecting species turnover and community composition, and in planning beyond the current range.

4. Integrating SDMs and TVAs

While SDM and TVA approaches may have different user groups and ultimate objectives (Table 2), both can inform conservation practitioners about which species should be prioritised for monitoring of climate change impacts. Similarly, both can inform species- and site-level adaptive management. However, for TVAs, this is primarily done at the species level, through identifying actions that may address the components of vulnerability that render each species vulnerable, and thus recommendations for site management may be generic rather than site-specific. SDM results can be applied at site and site-network scales, through projecting changes in range size and location. In addition, the potential turnover of species at individual sites can inform connectivity requirements between sites; recommendations for adaptive management are therefore capable of being specific for individual sites. When considered in the context of similar projections for all sites in a network, SDMs inform whether adaptation should be focused on maintaining persistence of currently occurring species or

Table 1
Examples of trait-based climate change vulnerability assessment approaches, the vulnerability traits they consider, and the species or groups to which they have been applied.

Approach	Dimensions of Vulnerability considered	Trait groups considered	Scale of documented application (numbers of species in brackets)
Foden et al. (2013)	Exposure, sensitivity, adaptive capacity	Habitat specialisation, environmental tolerances, interspecific interactions, reliance on environmental triggers, rarity, dispersal, evolvability, exposure	Global birds (9856), amphibians (6204), warm-water reef-building corals (797); other Central and East African species (1192)
Garnett et al. (2013)	Exposure, sensitivity, adaptive capacity	Specialisation (diet, habitats, foraging substrate, climate, brain size), reproductive capacity, genetic variability (population size), exposure	Australian birds (1237 taxa)
Gardali et al. (2012)	Exposure, sensitivity, adaptive capacity	Habitat specialisation, physiological tolerances; migratory status; dispersal ability, exposure	Californian birds (358)
Thomas et al. (2011)	Exposure, sensitivity, adaptive capacity	Rarity, interactions with other species, specific habitat-associated threats, other species-specific factors, exposure	UK butterflies (58), plants (18), bat (1), bird (1) and beetle (1) species
Graham et al. (2011)	Sensitivity	Diet specialisation, habitat specialisation, recruitment specialisation, body size	Coral reef fishes (134)
USFS-RMRS (Bagne et al., 2011)	Exposure, sensitivity, adaptive capacity	Habitat, physiology, phenology, biotic interactions, exposure	Designed for terrestrial vertebrates. Tested on a range of species from New Mexico, Arizona and Colorado
Chin et al. (2010)	Exposure, sensitivity, adaptive capacity	Rarity, habitat specificity, trophic specificity, immobility, physical/chemical intolerance, latitudinal range, exposure	Sharks and rays of the Great Barrier Reef (133)
NatureServe (Young et al., 2011)	Exposure, sensitivity, adaptive capacity	Dispersal, niche breadth, microhabitats, interspecific interactions, genetic factors and phenological response, exposure	Applied on an <i>ad hoc</i> basis to a range of N and S American species
EPA-NCEA (US EPA, 2009)	Baseline vulnerability and climate change vulnerability	Population and range sizes and trends, non-climate stresses & events, physiological vulnerability, habitat specialisation, dispersal ability, phenological dependency, interspecies dependency, exposure	North American birds (2), mammals (2), reptile (1) and fish (1)
Khaliq et al. (2014)	Exposure, sensitivity	Physiological tolerances, exposure	Birds (161) and mammals (297)

Table 2
Comparison of Species Distribution Models and Trait-based Vulnerability Assessments.

Method	SDMs	TVAs
Objective	To project future distribution of current climate types occupied by a species; to predict changing distribution of species' preferred climates	To identify those species most vulnerable to climate change, considering both climate exposure and species' traits
Methodological approach	Statistical association between species' distributions and contemporary climate, projected into the future	Identify traits associated with increased sensitivity and lower adaptive capacity to climate change for focal species group. Score each species based on possession of these traits and combine these scores with assessments of exposure to approximate overall vulnerability
Outputs	<ul style="list-style-type: none"> • Maps of projected distribution of suitable climates at different time-points (i.e. spatial and temporal patterns of distribution) for each species • Stacked-SDMs used to evaluate potential changes in community composition at a site- or local-scale 	<ul style="list-style-type: none"> • Ranks, categories, continuous scores or binary values for individual vulnerability components, used to derive a final vulnerability score • Stacked-TVAs can be used to show current concentrations/proportions of vulnerable species
Strengths	Produce spatially explicit maps of potential current and future distribution of suitable climate for individual species	Capture species' biological traits which are likely to play an important role in exacerbating or mitigating their climate change vulnerability
Limitations	<ul style="list-style-type: none"> • Do not consider non-climatic constraints on distribution, i.e. assume realised niche equates to fundamental niche, and climate-realised niche relationship will be maintained • Assume no local adaptation, behavioural responses, etc. • Generally unsuitable for species with small or unnaturally fragmented distribution ranges 	<ul style="list-style-type: none"> • Cannot easily be used to plan future management of areas not currently occupied by a species • Do not produce projections of species' future ranges or of community composition • Results are relative measures of vulnerability and limiting factors are difficult to identify • Require validation using observed species responses. Ignores local adaptation
Utility for identifying vulnerable species	Identify those species projected to undergo the greatest range change, and those with least overlap between current and projected distribution	Identify those species considered most vulnerable owing to greatest exposure and sensitivity, and least adaptive capacity
Utility for informing adaptive management	<ul style="list-style-type: none"> • Can inform priority-setting and guide appropriate responses at both a site scale, through identifying sites at which species management should be targeted, and also at a network scale • Identify key locations for action based on areas projected to retain or contain <i>de novo</i> species of conservation concern 	<ul style="list-style-type: none"> • Can inform priority-setting and guide appropriate responses for focal species through identifying the individual components of vulnerability • Identify key locations for action by highlighting broad areas containing highest concentrations/proportions of vulnerable species
Challenges for use in systematic conservation planning	<ul style="list-style-type: none"> • Robust climate projections are usually at too coarse a scale to inform systematic conservation planning, which often utilises fine-scale planning units • Areas that are climatically suitable for a species in future may not be colonised, which adds an inherent uncertainty in the systematic planning process that is difficult to quantify 	<ul style="list-style-type: none"> • Like SDMs, the scale of climate data limits utility in conservation planning • A lack of future projections of occupied sites makes future systematic planning near-impossible • Lack of spatially explicit species turnover makes application in dynamic spatial plans problematic • Outputs tend to be relative measures of vulnerability for particular focal species groups (e.g. amphibians or birds), but relative vulnerability between such groups cannot be inferred

facilitating colonisation of other species, or a balance between these two options (Hole et al., 2011).

We propose that by integrating both approaches, stronger and more robust climate change risk assessments for biodiversity can be made, and better – informed adaptation plans can be implemented. The advantages of an integrated approach are that it:

- (i) Could produce models (and consequently future projections) that better reflect the mechanisms by which species respond to climate change.
- (ii) Allows more biologically meaningful quantification of exposure to climate change, through using SDMs to identify which climatic variables are the best predictors of current distribution, and applying such exposure estimates to TVAs.
- (iii) Explicitly addresses many of the recognised inadequacies of each approach and the inconsistencies in the results that may be produced when they are applied separately.

Here we consider how each approach could be used to improve the other (as illustrated in the upper half of Fig. 2), and then discuss how SDMs and TVAs can be integrated into a single conceptual approach to conducting climate change vulnerability assessments and adaptive management planning (as illustrated in the lower half of Fig. 2). A recent paper by Pearson et al. (2014) utilised a

combination of SDM and traits to demonstrate how, jointly, they can inform extinction risk.

4.1. Incorporating information from TVAs into SDMs

There are a number of traits for which data are commonly collected through TVAs that could be usefully integrated into SDMs (see Fig. 2); such data include habitat preferences, intrinsic dispersal ability, extrinsic dispersal barriers, and environmental tolerances (e.g. to fire, flood, climate). Habitat preferences (a component of niche breadth) can be used to refine projections of present and future climate envelopes to give a more accurate estimate of realised niche (e.g. Boitani et al., 2007; Jetz et al., 2007; Rondinini et al., 2011) as well as environmental tolerances if adequate data are available. Such environmental tolerances might include known physiological limits for the focal species, or for other species on which it depends. Species' inherent dispersal abilities are not incorporated into traditional SDMs, but can be included in dynamic, iterative approaches, for example, by simulating range shifts using dispersal ability (e.g. Early and Sax, 2011; Barbet-Massin et al., 2012) and demographic processes (e.g. Willis et al., 2009b; Pearson et al., 2014).

Here we compare a basic SDM and TVA under a climate change scenario for two African bird species of conservation concern. We show how SDMs and TVAs can provide conflicting assessments of

potential impact and demonstrate how inclusion of traits into SDMs can improve threat assessments. SDM projections follow the methods of Baker et al. (2015), using end-of-century climate projections from a regional climate model from the Hadley Centre, UK (Buontempo et al., 2014). Future projections are produced in one of two ways. Firstly, we applied simple correlative SDMs to future climate projects. Secondly, to account for individual species traits, we considered dispersal ability and generation length, in addition to climate suitability, and used a gridded dispersal model with annual time-steps. The latter projections use the SDM to simulate climate suitability over time (changing climate suitability for cells every decade through the current century, based on mean annual suitability per decade) and permit species to expand (or contract) their range according to their ability to disperse to climatically suitable cells within their dispersal capability at each generation time step (simulated using MigClim; Engler et al., 2012). TVA assessments come from Foden et al. (2013).

An example of a species for which assessments could be made more accurate by the inclusion of trait data into SDMs is the White-necked Picathartes (*Picathartes gymnocephalus*). A basic SDM projects this species to have the potential to increase its current distribution size by about 600% by the end of this century (Fig. 1a). A TVA suggests this species has low climate change vulnerability due to low climate exposure. However, the exposure metric from the SDM suggests approximately 50% of its current range will be climatically unsuitable in future. Incorporating the species' low dispersal ability (with a likely mean dispersal distance per generation of just a few kilometres (BirdLife International, unpublished data) into a dynamic SDM indicates also that it will be unable to colonise areas with newly suitable climate, and is probably more vulnerable to climate change than either the basic SDM or TVA suggest individually.

In the case of the related Grey-necked Picathartes (*Picathartes oreas*, Fig. 1b), a TVA suggests 'high' exposure to climate change, whereas SDM projections suggest that changing climate suitability within its current range is similar to that experienced by *P. gymnocephalus* (ca. 50% reduction of suitable climate within the current range in both cases). A dynamic SDM suggests some potential for range expansion beyond its current range. However, in both cases

the TVAs highlight that the species have low adaptive capacities due to specialised habitat requirements (a requirement for rock-faces, cliffs, or cave roofs and walls for nesting), something the dynamic SDMs in Fig. 1 do not consider. As a result of their breeding specialisation, both species are unlikely to colonise most newly climatically suitable areas. These two examples provide some indication of how SDMs and TVAs, when considered in isolation, can provide incomplete (and therefore inaccurate) assessments of potential impacts.

To determine if extrinsic barriers to species' dispersal exist, species habitat preferences can be used alongside current and projected land use to assess connectivity between current and projected future ranges. However, projections of future land use are currently limited: they are often only available at coarse spatial resolutions and are prone to considerable uncertainties. Notwithstanding these challenges, such data could be used to 'clip' projected future suitable climatic areas, taking into account other factors such as altitude and very specialised habitat requirements. Climate itself can prove a dispersal barrier if it limits a species response rate over time. For this reason dynamic dispersal models that include temporal alterations in climate suitability will improve projections of future occupancy (e.g. Early and Sax, 2011). Other potential dispersal barriers such as mountains, oceans or rivers are also not typically incorporated into traditional SDM approaches, which can lead to over-projections of species distribution expansions. For example, a failure to account for dispersal barriers in the Tanzanian Eastern Arc Mountains would have resulted in over-projection of range shifts of endemic plant species (Platts et al., 2013). Such barriers could be considered *post hoc* to limit the extent of potential future range. Alternatively, such barriers could be used *a priori* to define the limits of the modelled area that the species could expand into.

Refining SDMs with traits can identify: species and areas in need of more protection, the likely limiting factors for adaptation, and the key factors affecting species sensitivity. As a result, such models can inform management actions and permit mapping of, for example, climate refugia, hotspots of potential species losses, overall species turnover and potential areas for colonisation. Some traits currently considered in TVAs are probably not suitable

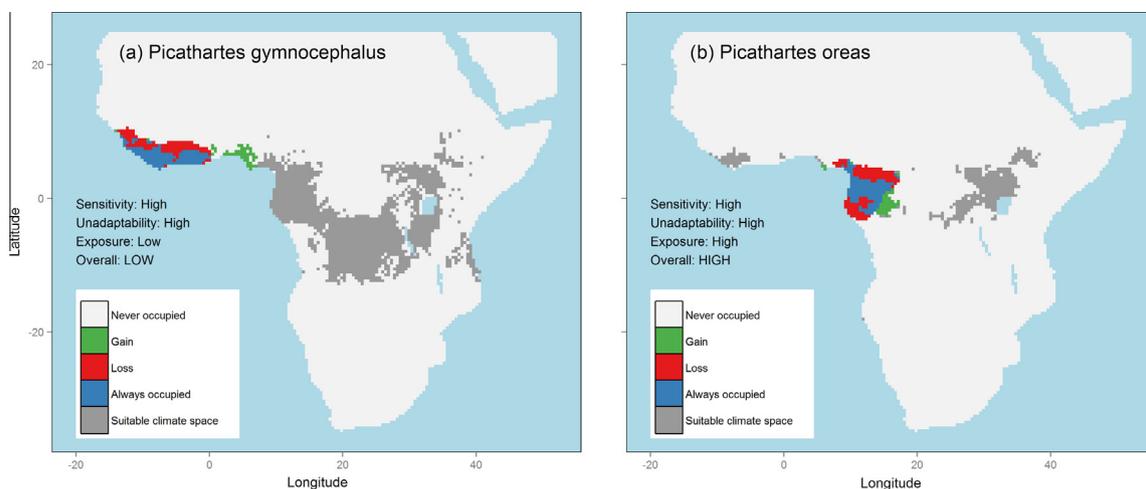


Fig. 1. Climate change vulnerability over the current century as assessed by simple SDMs and corresponding dynamic dispersal models; the latter considering changing climate suitability from SDMs along with dispersal-related traits (mean dispersal distance and generation length) from TVAs. Text within maps gives the TVA scores for sensitivity, low adaptive capacity, exposure and overall vulnerability for each species (from Foden et al., 2013). Figures show changes in simulated areas of occurrence (from SDMs) for two African bird species of current conservation concern: (a) White-necked Picathartes, *Picathartes gymnocephalus* and (b), Grey-necked Picathartes, *Picathartes oreas* between the present and 2100. Blue shading indicates climate suitability in both periods, green indicates areas becoming newly suitable by 2100 and within the species' dispersal capability over that period. Red indicates areas becoming unsuitable over the period, and grey indicates areas that are climatically suitable by 2100 (from the simple SDM) but beyond the species' dispersal capability during the period. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

for incorporation into SDMs for many species at present, but could be useful in providing insights into exacerbating factors in relation to projected changes in climatic suitability. Such traits include microhabitat affiliations, environmental tolerances (other than direct climate effects), complex interspecific interactions and the potential for micro-evolution or behavioural adaptation.

4.2. Incorporating information from SDMs into TVAs

A number of elements from SDMs could be incorporated into TVAs. Narrow climatic tolerances, a trait commonly considered when assessing sensitivity (see Fig. 2 for traits framework), might be better informed by data from SDMs that quantify the breadth of

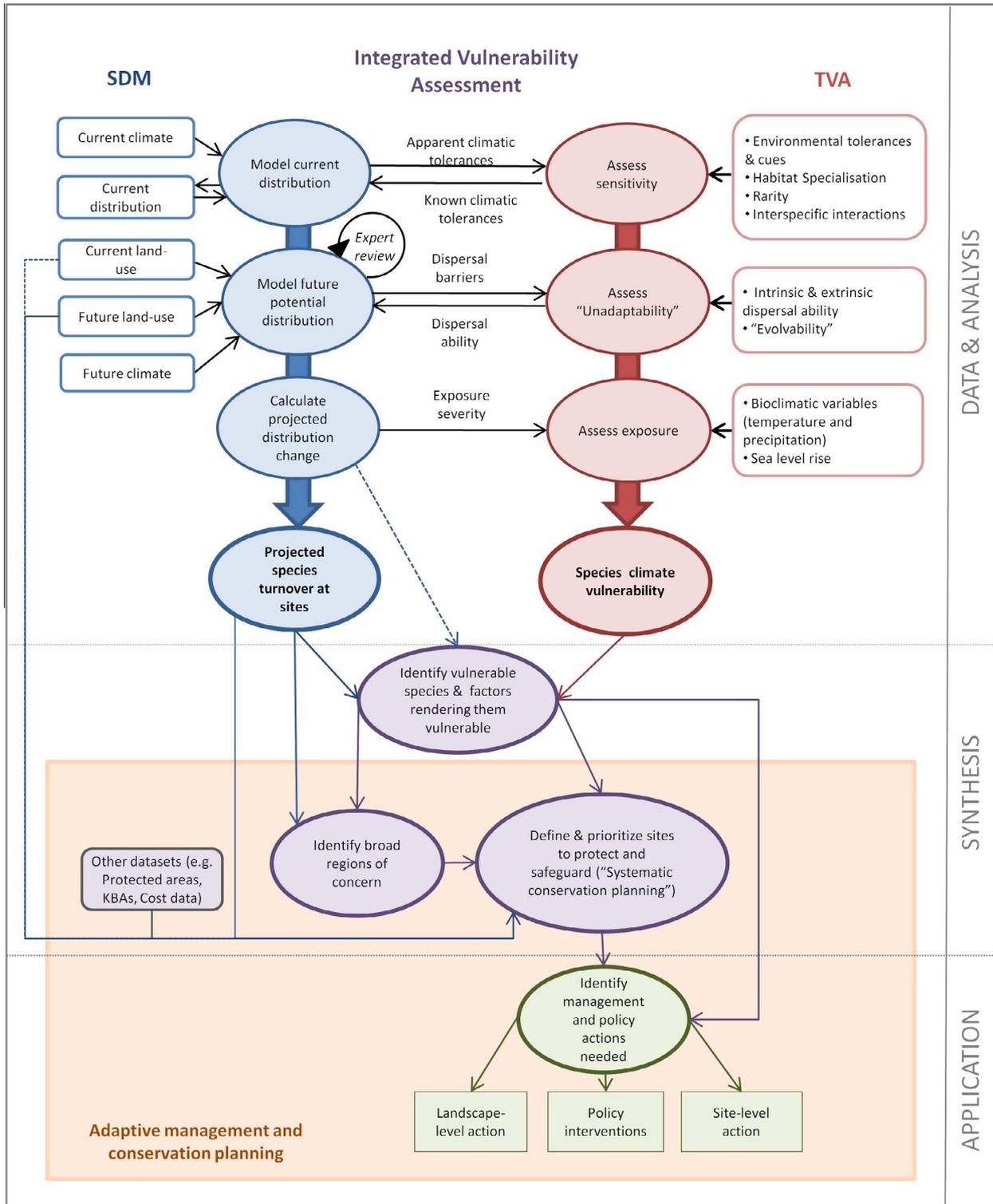


Fig. 2. Conceptual model demonstrating potential ways to integrate SDM and TVA approaches, as well as their links to systematic conservation planning and adaptive management.

a species' multi-dimensional climate niche, assuming that the currently utilised areas reflect real climatic limits. When multiple climatic variables can be tested in model selection, and where detailed species distribution data are available, SDMs could also be used to identify the climatic variables that are most important for determining the current distribution of a species (Feeley et al., 2012). This would enable species-specific choices of the most relevant climate variables for assessment of climate change sensitivity and exposure.

TVAs often consider vulnerability associated with dispersal in terms of both species' intrinsic abilities (mean and maximum dispersal distances under current natural conditions) and extrinsic opportunity (e.g. the presence of dispersal barriers such as sea, rivers or intervening land at altitudes that are not tolerated), and tend to make generalised assumptions about suitable future climate space requirements in areas of increasing latitude and/or altitude. SDMs could be used to identify more accurately the availability and location of suitable climatic conditions at various points in time in the future, thereby informing whether species' inherent dispersal abilities and/or their extrinsic barriers are likely to prevent the species from successfully tracking climate shifts (as in Fig. 1). SDMs applied to future climates could be used either directly to estimate exposure (change in suitability), or to identify thresholds for climate suitability to estimate, for example, the percentage of species' current distribution ranges that will experience climatic conditions outside the ranges they currently experience.

Incorporating information from SDMs into TVAs will provide refined TVAs. However, the resultant outputs remain scores of relative vulnerability, which, whilst very useful for flagging species (and hotspots of species) of particular vulnerability, may have more limited utility in planning adaptation strategies. For this reason, we advocate a fully integrative approach that combines SDMs and TVAs to provide output of maximum value for adaptation planning (Fig. 2). We provide worked examples of a potential integrative approach in the following section.

5. Integrating SDM and TVA outputs into climate change vulnerability assessment and adaptation planning

5.1. Identifying vulnerable species and broad regions of concern

Both SDM and TVA approaches can be used to identify species that may be of concern in the future owing to their vulnerability to some aspects of climate change. However, each approach currently achieves this through the analysis of different input data, and provision of different outputs. While SDMs explicitly identify species projected to lose (or gain) apparently suitable climate space, TVAs highlight species that are expected to experience change across their current distribution, and then consider the mechanism(s) through which this might impact upon the species of interest; TVAs take no account of potential future range changes. In our integrative framework, traits that can be quantified (as continuous measures rather than scores) are implicitly incorporated into dynamic SDM models to refine range dynamics (as occurs with dispersal and generation length in the model outputs shown in Fig. 1). In addition to dispersal ability and generation length, such traits might also include, habitat preferences, population size (Howard et al., 2014), species interactions (Mason et al., 2014) and population dynamics and interactions (Guisan and Rahbek, 2011). Other traits considered in TVAs can be accounted for spatially in refinements to dynamic SDMs, e.g. dispersal barriers. This integrative approach is entirely quantitative and spatially explicit and addresses the individual caveats of both approaches. Recent examples of such integrative approaches include simulations of future threats to European birds (Barbet-Massin et al.,

2012) and to American mammals (Schloss et al., 2012), and reach their most integrated in spatially explicit metapopulation models (Pearson et al., 2014) that use several of the life history traits typically used in TVAs.

Here we propose a simple procedure (Fig. 3) that allows for the integration of traits that cannot be directly incorporated into SDM modelling frameworks to provide simple management recommendations. This approach utilises, as a starting point, the best available projections from integrated SDM–TVA models but externalises and considers complex additional factors subsequently, prior to producing an outline management recommendation for individual species. Following the flow chart in Fig. 3 for the case of the White-necked Picathartes example given above, eventually (Table 3) leads to the question 'Is a species/habitat on which the focal species relies differentially impacted?' The interacting habitat in this case is cliff-face breeding locations, which are climate insensitive, so the main recommendation would be to prioritise sites of future co-occurrence of the bird and its nesting habitat. Table 3 shows further indicative management suggestions for a small subset of West African birds for which dynamic SDM and TVA assessments were made (see Supplementary Fig. S1 for equivalent maps to those provide for the two *Picathartes* species in Fig. 1).

However, the *Picathartes* examples also demonstrate a problem with applying simple rules to complex problems, as nesting sites are likely to be only one important interacting factor (for example, these two species feed at army ant swarms, whose occurrence might also be impacted by climate change). Knowledge of complex potential limiting factors is likely to be poorly understood for the majority of species globally; even for very well-studied species, understanding the drivers of recent population changes can take decades of research. Consider, for example, the research needed to elucidate the impacts of pesticides on raptors (Hickey and Anderson, 1968), or to deduce indirect (Visser and Both, 2005) or direct climatic impacts on songbirds (Robinson et al., 2004). Added complexity also occurs when species are migratory; in such cases the questions in Fig. 3 could be applied separately to the breeding range, non-breeding range and passage range. All of the above suggests that generalising management actions for many species using simple rules could be misinformative. A better approach might be to use integrated SDM and trait data to flag potentially vulnerable species and to then consider each species in greater detail. Such an approach has been adopted to develop climate change adaptation plans for Australian birds (Garnett and Franklin, 2014) and this approach exemplifies, in our opinion, the best way by which to plan for climate impacts on biodiversity while also considering the many potential uncertainties in climate data, trait data and modelling practices.

5.2. Adaptive management planning: identifying sites to protect and safeguard

Spatial conservation prioritisation is the process of identifying networks of important sites for meeting conservation goals, and planners increasingly aim for these networks to mitigate the impacts of climate change (Hole et al., 2009, 2011; Game et al., 2011). The first step in this process is identifying the species and habitats that should be included in these networks; integrated SDM–TVA approaches can play an important role in this process, as they help identify vulnerable species for inclusion in the prioritisation scheme. In addition, they can be used to help set representation targets, as it is common to set higher targets for more vulnerable species (Pressey et al., 2003), and to develop guidance on the minimum size or spacing of sites and connectivity between sites (Smith et al., 2010; Moffitt et al., 2011). Beyond identifying species likely to be most vulnerable to climate change, and thereby informing prioritisation for species management, integrated SDM–

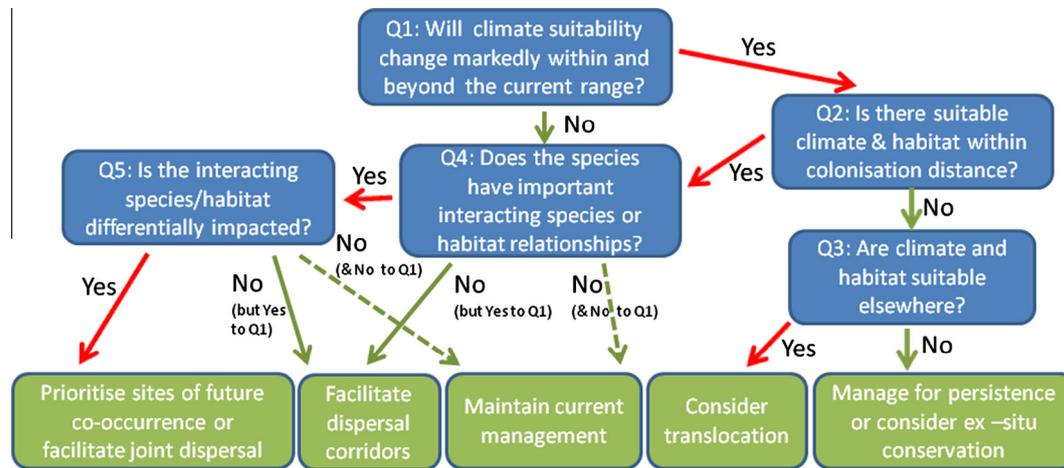


Fig. 3. Flow chart demonstrating the potential for integration of SDM and TVA approaches in practice. Blue boxes are questions answered from SDM and TVA data; Q1–Q3 can be answered from integrated SDM–TVA models and Q4–Q5 from *post hoc* trait considerations. Green boxes indicate the resultant management actions to consider, in addition to continued management within the current range. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

TVA approaches can also indicate regions where vulnerable species are concentrated. Prevalence of particular vulnerability traits for individual species or species groups, or traits that occur in particular areas can provide insight into effective conservation interventions. For example, for species that face high exposure and have good inherent dispersal ability but face extrinsic barriers to dispersal (Dawson et al., 2011; Foden et al., 2013), it may be feasible to increase barrier permeability, or to plan for assisted colonisation (Hoegh-Guldberg et al., 2008; Willis et al., 2009a), while for areas containing high proportions of species that are sensitive due to particular traits (e.g. low salinity or drought tolerance), appropriate site or regional scale actions can be taken.

Integrated models can play a key role in future-proofed spatial prioritisation, and techniques are available to account for the inevitable uncertainty in the projected suitability maps (Carvalho et al., 2011; Bagchi et al., 2013). One approach is to select only those individual sites that are important for conserving both the current and projected future distributions of species (i.e. sites in which species are projected to persist). However, this is obviously problematic for species with projected future distributions that do not overlap with their current range and this approach could also lead to low priority being given to sites that are projected to be critical in the future for new communities of species. Instead, integrated models can be used to identify locations outside such networks that may be priorities to add to the existing networks, given the projected loss of species in existing sites (e.g. Hole et al., 2009). Moreover, for species projected to need to alter their range in future, planners can specify species-specific maximum distances between current and future sites with suitable habitat, based on the dispersal estimates used in TVAs (Carroll et al., 2010; Summers et al., 2012).

5.3. Adaptive management planning: identifying management actions needed

Adaptive management is crucial in conservation that is cognisant of climate change, since future range shifts, and indeed future climate change, may not follow model projections. Similarly, understanding of the intrinsic and extrinsic traits that make species vulnerable to climate change may change over time, as unconsidered limitations (or opportunities) come to light. In addition to helping to design protected area (or conservation site) networks, integrated models can inform the management actions

needed for climate change adaptation. Traits can be used to help identify the actions that may address those components of vulnerability that render each species vulnerable. For example, identification of a species whose persistence is dependent upon a specific habitat (or some component thereof), that itself might be altered under climate change (e.g. the drying of a wetland) might result in efforts to actively manage the habitat for the benefit of the species (e.g. water course management). Similarly, persistence may depend on another species (e.g. an essential pollinator or prey species), which requires co-management with the species of concern. Alternatively, a species identified as being unable to disperse to a newly suitable location (due to either intrinsic or extrinsic factors) might highlight a requirement to assist the colonisation of this species at a new location.

Dynamic SDMs can be used to project the turnover of species at sites and potentially also its timing, as well to project individual species range changes, to identify the locations of climatic refugia and limiting factors to colonisation, and to compare potential range shifts to projected climate velocities. However, lags in colonisation of areas that become climatically suitable and extinction debts are both difficult to predict. When considered in the context of similar projections for all sites in a network, such information can be used to decide whether adaptation at particular sites should be focused at any point on maintaining persistence of currently occurring species, or facilitating colonisation of other species, or a balance between these two options. In such situations monitoring will be crucial to determining whether changes are occurring as projected, and whether adaptation to management plans for site networks is necessary.

5.4. Considerations of spatial resolution and uncertainty

When conservation planning is undertaken using future climate projections, the spatial resolution of the climate data may become a limiting factor to conservation decision-making (Tabor and Williams, 2010; Wiens and Bachelet, 2010). While higher resolution climate projections (e.g. down to 1 km²) for current and future periods do exist (e.g. Kendon et al., 2012), they have inherent uncertainties arising from the extrapolation and statistical down-scaling used in their production; an ensemble approach to future climate prediction at the regional scale is only feasible at spatial scales of ca. 25–50 km (Giorgi et al., 2009; Nikulin et al., 2012). At this scale, the conservation planning will be relatively

Table 3
Potential management actions (in addition to maintaining management at sites within the current range that are projected to remain climatically suitable) for ten West African endemic bird species, informed by integrating SDM and TVA data. Q1–Q5 in column headings refer to the five questions in the flow chart in Fig. 3, which result in the management recommendations provided in the final column.

Scientific name	Common name	Habitat use and interspecific interactions	Q1-Climate change?	Q2-Colonisable habitat?	Q3-Distant habitat?	Q4-Interacting species?	Q5-Differing responses for focal and interacting species?	Management Recommendation
<i>Picathartes gymnocephalus</i>	White-necked picathartes	Rocky rainforest areas and streams at high altitude; can follow army ants; poor disperser	Yes	Yes (within range); no (beyond)	Yes	Yes	Yes	Consider translocations
<i>Picathartes oreas</i>	Grey-necked picathartes	Rocky rainforest areas and streams; can follow army ants	Yes	Yes	–	Yes	Yes	Facilitate dispersal to sites with suitable habitat
<i>Crinifer piscator</i>	Western grey plantain-eater	Open woodland; frugivore	No (within); yes (beyond)	Yes	–	No and no	–	Maintain current population and facilitate movement
<i>Bycanistes cylindricus</i>	Brown-cheeked hornbill	Primary forest; large emergent trees for nests	Yes	Yes	–	Yes	No (suitable primary forest already exists beyond range)	Facilitate dispersal corridors
<i>Musophaga violacea</i>	Violet turaco	Forests; frugivorous	No (within); yes (beyond)	No (beyond) (suitable area sahelian scrub)	No (beyond range)	No	–	Maintain current management
<i>Agelastes meleagrides</i>	White-breasted guineafowl	Primary and old secondary forest; shy	Yes	Yes	–	No	–	Facilitate dispersal corridors
<i>Scotopelia ussheri</i>	Rufous fishing owl	Riverine forest habitats	Yes	Yes	–	Yes	Possibly (aquatic prey)	Prioritise sites of co-occurrence, or facilitate dispersal of both
<i>Telacanthur melanopygia</i>	Black (Chapin's) spinetail	Above forest canopy and cliffs in forests	Yes	No	No	–	–	Manage for persistence
<i>Lybius dubius</i>	Bearded barbet	Generalist woodland frugivore and insectivore	No (within); yes (beyond)	No (beyond) (suitable area sahelian scrub)	No (beyond range)	No	–	Maintain current management
<i>Dendropicos elachus</i>	Little grey woodpecker	Dry sahelian woodland along watercourses	Yes	Yes (new range has suitable habitat)	–	No	–	Facilitate dispersal corridors

coarse, and larger than many protected areas or remaining habitat patches. Additionally, many species of conservation concern occur only in restricted microclimatic regions, for example beneath rain-forest canopies, in river gorges, beside waterfall spray zones, or dependent on small seasonal wetlands that are poorly represented by mean climate that is not mediated by local vegetation or topography and is mapped at a coarse scale.

Additional inputs required for future conservation planning, such as projections of land cover/use and human population density/distribution, are also difficult to produce. Consequently, making projections of species and habitat change into the future, and using these for conservation planning at the national or sub-national scale, require careful choices of appropriate methods and data, and careful interpretation of results. It is vital to understand the uncertainties inherent in the underlying data that contribute to both SDM and TVA assessments, and to quantify or quantify these uncertainties (Bagchi et al., 2013; Baker et al., 2015). Only by thoroughly testing these integrated approaches on past changes (e.g. hind-casting, Green et al., 2008) can we have confidence in their potential future utility.

SDMs and TVAs, either considered separately or when integrated, can provide valuable information for systematic conservation planning when looking at future conservation needs. Information from integrated models on potential future ranges of species can be used to prioritise future sites for protection, and the likelihood of occurrence can even be used as a weighting factor in site selection (Carvalho et al., 2011). For species that need to alter their range in a particular direction, or for those with limited dispersal capacity, sites within the required area/distance could be prioritised in plans. Habitats and microclimates upon which particular species have high dependency or specialisation as identified in TVAs, can be incorporated into requirements for planning units. When considering systematic conservation plans for multiple species, prioritisation could be given to those species that have been identified as particularly vulnerable to climate change. However, to date, most systematic planning has been static, focussed on a single time period. One of the major challenges for systematic conservation planning under climate change will be how to schedule conservation effort and site selection over both space and time, to enable the persistence of species during periods of change.

6. Summary

Here we present a framework that brings together SDMs and TVAs for species-level climate change vulnerability assessments. Such approaches, integrating climate and trait information are becoming more widely used (Sinervo et al., 2010; Pearson et al., 2014). We propose how these integrated approaches can feed into adaptation planning, but caution that their use in systematic conservation planning requires consideration of the inherent uncertainties in the many projections of future change required (Wiens and Bachelet, 2010). We suggest that future planning using SDMs and TVAs should only be undertaken in light of informed expert knowledge for individual species and habitats. Integrating these approaches will also provide useful information for actions beyond planning; they can inform the selection of sites and species for monitoring, as well as the specific actions taken to conserve the species occurring at sites. It is essential that systematic monitoring is established to verify the temporal and spatial pattern of projections, to validate their incorporation into conservation planning and to monitor the effectiveness of adaptive interventions.

Acknowledgments

We thank the UNEP DEPI/GEF PARCC (Protected Areas Resilient to Climate Change) West Africa project for funding the two day

workshop in Cambridge that provided the basis for this paper. The authors all acknowledge the support of their institutions for the time to work on this paper.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2015.05.001>.

References

- Araújo, M.B., Alagador, D., Cabeza, M., Nogués-Bravo, D., Thuiller, W., 2011. Climate change threatens European conservation areas. *Ecol. Lett.* 14, 484–492.
- Araújo, M.B., Ferri-Yáñez, F., Bozinovic, F., Marquet, P.A., Valladares, F., Chown, S.L., 2013. Heat freezes niche evolution. *Ecol. Lett.* 16, 1206–1219.
- Bagchi, R., Crosby, M., Huntley, B., Hole, D.G., Butchart, S.H.M., Collingham, Y.C., Kalra, M., Rajkumar, J., Rahmani, A., Pandey, M., Gurung, H., Trai, L.T., Van Quang, N., Willis, S.G., 2013. Evaluating the effectiveness of conservation site networks under climate change: accounting for uncertainty. *Glob. Change Biol.* 19, 1236–1248.
- Bagne, K.E., Friggens, M.M., Finch, D.M., 2011. A System for Assessing Vulnerability of Species (SAVS) to Climate Change. Gen. Tech. Rep. RMRS-GTR-257. Fort Collins, CO. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 28.
- Baker, D.J., Hartley, A.J., Burgess, N.D., Butchart, S.H.M., Carr, J.A., Smith, R.J., Belle, E., Willis, S.G., 2015. Assessing climate change impacts for vertebrate fauna across the West Africa protected area network using regionally appropriate climate projections. *Divers. Distrib.* <http://dx.doi.org/10.1111/ddi.12337>.
- Barbet-Massin, M., Thuiller, W., Jiguet, F., 2012. The fate of European breeding birds under climate, land-use and dispersal scenarios. *Glob. Change Biol.* 18, 881–890.
- Beaumont, L.J., Hughes, L., 2002. Potential changes in the distributions of latitudinally restricted Australian butterfly species in response to climate change. *Glob. Change Biol.* 8, 954–971.
- Benning, T.L., LaPointe, D., Atkinson, C.T., Vitousek, P.M., 2002. Interactions of climate change with biological invasions and land use in the Hawaiian Islands: modeling the fate of endemic birds using a geographic information system. *Proc. Natl. Acad. Sci. USA* 99, 14246–14249.
- Boitani, L., Falcucci, A., Maiorano, L., Rondinini, C., 2007. Ecological networks as conceptual frameworks or operational tools in conservation. *Conserv. Biol.* 21, 1414–1422.
- Buontempo, C., Mathison, C., Jones, R., Williams, K., Wang, C., McSweeney, C., 2014. An ensemble climate projection for Africa. *Clim. Dyn.* <http://dx.doi.org/10.1007/s00382-014-2286-2>.
- Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E.E., Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., Carr, G.M., Chanson, J., Chenery, A.M., Csirke, J., Davidson, N.C., Dentene, R.F., Foster, M., Galli, A., Galloway, J.N., Genovesi, P., Gregory, R.D., Hockings, M., K.V., Lamarque, J.-F., Leverington, F., Loh, J., McGeoch, M.A., McRae, L., Minasyan, A., Morcillo, M.H., Oldfield, T.E.E., Pauly, D., Quader, S., Revenga, C., Sauer, J.R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S.N., Symes, A., Tierney, M., Tyrrell, T.D., Vié, J.C., Watson, R., 2010. Global biodiversity: indicators of recent declines. *Science* 328, 1164–1168.
- Carroll, C., Dunk, J.R., Moilanen, A., 2010. Optimizing resiliency of reserve networks to climate change: multispecies conservation planning in the Pacific Northwest, USA. *Glob. Change Biol.* 16, 891–904.
- Carvalho, S.B., Brito, J.C., Crespo, E.G., Watts, M.E., Possingham, H.P., 2011. Conservation planning under climate change: toward accounting for uncertainty in predicted species distributions to increase confidence in conservation investments in space and time. *Biol. Conserv.* 144, 2020–2030.
- Chin, A., Kyne, P., Walker, T.I., McAuley, R.B., 2010. An integrated risk assessment for climate change: analysing the vulnerability of sharks and rays on Australia's Great Barrier Reef. *Glob. Change Biol.* 16, 1936–1953.
- Coetzee, B.W.T., Robertson, M.P., Erasmus, B.F.N., van Rensburg, B.J., Thuiller, W., 2009. Ensemble models predict important bird areas in southern Africa to become less effective for conserving endemic birds under climate change. *Glob. Ecol. Biogeogr.* 18, 701–710.
- Conlisk, E., Syphard, A.D., Franklin, J., Flint, L., Flint, A., Regan, H., 2013. Uncertainty in assessing the impacts of global change with coupled dynamic species distribution and population models. *Glob. Change Biol.* 19, 858–869.
- Dawson, T.P., Jackson, S.T., House, J.I., Prentice, I.C., Mace, G.M., 2011. Beyond predictions: biodiversity conservation in a changing climate. *Science* 332, 53–58.
- Early, R., Sax, D.F., 2011. Climate-path analysis reveals potential limitations on species range shifts. *Ecol. Lett.* 14, 1125–1133.
- Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, C., Nakazawa, Y., Overton, J.M.M., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S., Wisz, M.S., Zimmermann, N.E., 2006. Novel methods improve

- prediction of species' distributions from occurrence data. *Ecography* 29, 129–151.
- Engler, R., Hordijk, W., Guisan, A., 2012. The MIGCLIM R package – seamless integration of dispersal constraints into projections of species distribution models. *Ecography* 35, 872–878.
- Feeley, K.J., Malhi, Y., Zelazowski, P., Silman, M.R., 2012. The relative importance of deforestation, precipitation change, and temperature sensitivity in determining the future distributions and diversity of Amazonian plant species. *Glob. Change Biol.* 18, 2636–2647.
- Foden, W.B., Butchart, S.H.M., Stuart, S.N., Vié, J.-C., Akçakaya, H.R., Angulo, A., DeVantier, L.M., Gutsche, A., Turak, E., Cao, L., Donner, S.D., Katariya, V., Bernard, R., Holland, R.A., Hughes, A.F., O'Hanlon, S.E., Garnett, S.T., Şekercioglu, Ç.H., Mace, G.M., 2013. Climate change susceptibility of the world's birds, amphibians and corals. *PLoS ONE* 8, e65427.
- Game, E.T., Lipsett-Moore, G., Saxon, E., Peterson, N., Sheppard, S., 2011. Incorporating climate change adaptation into national conservation assessments. *Glob. Change Biol.* 17, 3150–3160.
- García, R.A., Burgess, N.D., Cabeza, M., Rahbek, C., Araújo, M.B., 2012. Exploring consensus in 21st century projections of climatically suitable areas for African vertebrates. *Glob. Change Biol.* 18, 1253–1269.
- García, R.A., Araújo, M.B., Burgess, N.D., Foden, W.B., Gutsche, A., Rahbek, C., Cabeza, M., 2014. Matching species traits to projected threats and opportunities from climate change. *J. Biogeogr.* 41, 724–735.
- Gardali, T., Seavy, N.E., DiGaudio, R.T., Comrack, L.A., 2012. A climate change vulnerability assessment of California's at-risk birds. *PLoS ONE* 7, e29507.
- Garnett, S.T., Franklin, D.C. (Eds.), 2014. *Climate Change Adaptation Plans for Australian Birds*. CSIRO, Collingwood, Australia.
- Garnett, S.T., Franklin, D.C., Ehmke, G., VanDerWal, J.J., Hodgson, L., Pavey, C., Reside, A.E., Welbergen, J.A., Butchart, S.H.M., Perkins, G.C., Williams, S.E., 2013. *Climate Change Adaptation Strategies for Australian Birds*. National Climate Change Adaptation Research Facility, Gold Coast.
- Giorgi, F., Jones, C., Asrar, G.R., 2009. Addressing climate information needs at the regional level: the CORDEX framework. *WMO Bull.* 58, 175–183.
- Graham, N.A.J., Chabanet, P., Evans, R.D., Jennings, S., Letourneur, Y., MacNeil, M.A., McClanahan, T.R., Ohman, M.C., Polunin, N.V.C., Wilson, S.K., 2011. Extinction vulnerability of coral reef fishes. *Ecol. Lett.* 14, 341–348.
- Green, R.E., Collingham, Y.C., Willis, S.G., Gregory, R.D., Smith, K.W., Huntley, B., 2008. Performance of climate envelope models in retrodicting recent changes in bird populations from observed climatic change. *Biol. Lett.* 4, 599–602.
- Gregory, R.D., Willis, S.G., Jiguet, F., Voříšek, P., Klvaňová, A., 2009. An indicator of the impact of climatic change on European bird populations. *PLoS ONE* 4, e4678.
- Guisan, A., Rahbek, C., 2011. SESAM – a new framework integrating macroecological and species distribution models for predicting spatio-temporal patterns of species assemblages. *J. Biogeogr.* 38, 1433–1444.
- Harrison, P.A., Berry, P.M., Butt, N., New, M., 2006. Modelling climate change impacts on species' distributions at the European scale: implications for conservation policy. *Environ. Sci. Policy* 9, 116–128.
- Hickey, J.J., Anderson, D.W., 1968. Chlorinated hydrocarbons and eggshell changes in raptorial and fish-eating birds. *Science* 162, 271–273.
- Hoegh-Guldberg, O., Hughes, L., McIntyre, S., Lindenmayer, D.B., Parmesan, C., Possingham, H.P., Thomas, C.D., 2008. Assisted colonization and rapid climate change. *Nature* 321, 345–346.
- Hof, C., Araujo, M.B., Jetz, W., Rahbek, C., 2011. Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature* 480, 516–U137.
- Hole, D.G., Willis, S.G., Pain, D.J., Fishpool, L.D., Butchart, S.H.M., Collingham, Y.C., Rahbek, C., Huntley, B., 2009. Projected impacts of climate change on a continent-wide protected area network. *Ecol. Lett.* 12, 420–431.
- Hole, D.G., Huntley, B., Arinaitwe, J., Butchart, S.H.M., Collingham, Y.C., Fishpool, L.D.C., Pain, D.J., Willis, S.G., 2011. Toward a management framework for networks of protected areas in the face of climate change. *Conserv. Biol.* 25, 305–315.
- Howard, C., Stephens, P.A., Pearce-Higgins, J.W., Gregory, R.D., Willis, S.G., 2014. Improving species distribution models: the value of data on abundance. *Methods Ecol. Evol.* 5, 506–513.
- Huntley, B., Collingham, Y.C., Willis, S.G., Green, R.E., 2008. Potential impacts of climatic change on European breeding birds. *PLoS ONE*, 3.
- IPCC, 2007. *Climate change 2007: the physical science basis. Contribution of working group I to the fourth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK, and New York, NY, USA.
- Jensen, R.A., Madsen, J., O'Connell, M., Wisz, M.S., Tommervik, H., Mehlum, F., 2008. Prediction of the distribution of Arctic-nesting pink-footed geese under a warmer climate scenario. *Glob. Change Biol.* 14, 1–10.
- Jetz, W., Wilcove, D.S., Dobson, A.P., 2007. Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biol.* 5, 1211–1219.
- Kearney, M., Porter, W., 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecol. Lett.* 12, 334–350.
- Kendon, E.J., Roberts, N.M., Senior, C.A., Roberts, M.J., 2012. Realism of rainfall in a very high-resolution regional climate model. *J. Clim.* 25, 5791–5806.
- Khaliq, I., Hof, C., Prininger, R., Böhning-Gaese, K., Pfenninger, M., 2014. Global variation in thermal tolerances and vulnerability of endotherms to climate change. *Proc. Royal Soc. B*. <http://dx.doi.org/10.1098/rspb.2014.1097>.
- Ladle, R.J., Whittaker, R.J., Watson, J.E.M., Grantham, H.S., Wilson, K.A., Possingham, H.P., 2011. Systematic conservation planning: past, present and future. In: Ladle, R.J., Whittaker, R.J. (Eds.), *Conservation Biogeography*. Blackwells, Oxford, UK.
- Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. *Nature* 405, 243–253.
- Mason, T.H.E., Stephens, P.A., Apollonio, M., Willis, S.G., 2014. Predicting potential responses to future climate in an alpine ungulate: interspecific interactions exceed climate effects. *Glob. Change Biol.* 20, 3872–3882.
- Midgley, G.F., Hannah, L., Millar, D., Rutherford, M.C., Powrie, L.W., 2002. Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Ecol. Biogeogr.* 11, 445–451.
- Moffitt, E.A., White, J.W., Botsford, L.W., 2011. The utility and limitations of size and spacing guidelines for designing marine protected area (MPA) networks. *Biol. Conserv.* 144, 306–318.
- Moilanen, A., Wilson, K.A., Possingham, H.P., 2009. *Spatial Conservation Prioritization: Quantitative Methods and Computational Tools*. Oxford University Press, Oxford, UK.
- Nikulin, G., Jones, C., Giorgi, F., Asrar, G., Buechner, M., Cerezo-Mota, R., Christensen, O.B., Deque, M., Fernandez, J., Haensler, A., van Meijgaard, E., Samuelsson, P., Sylla, M.B., Sushama, L., 2012. Precipitation climatology in an ensemble of CORDEX-Africa regional climate simulations. *J. Clim.* 25, 6057–6078.
- Pacifici, M., Foden, W.B., Visconti, P., Watson, J.E.M., Butchart, S.H.M., Kovacs, K.M., Scheffers, B.R., Hole, D.G., Martin, T.G., Akçakaya, H.R., Corlett, R.T., Huntley, B., Bickford, D., Carr, J.A., Hoffmann, A.A., Midgley, G.F., Pearce-Kelly, P., Pearson, R.G., Williams, S.E., Willis, S.G., Young, B., Rondinini, C., 2015. Assessing species vulnerability to climate change. *Nat. Clim. Change* 5, 215–224.
- Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37–42.
- Pearson, R.G., Dawson, T.P., 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Glob. Ecol. Biogeogr.* 12, 361–371.
- Pearson, R.G., Stanton, J.C., Shoemaker, K.T., Aiello-Lammens, M.E., Ersts, P.J., Horning, N., Fordham, D.A., Raxworthy, C.J., Ryu, H.Y., McNeese, J., Akçakaya, H.R., 2014. Life history and spatial traits predict extinction risk due to climate change. *Nat. Clim. Change* 4, 217–221.
- Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. *Ecol. Model.* 190, 231–259.
- Platts, P.J., Gereau, R.E., Burgess, N.D., Marchant, R., 2013. Spatial heterogeneity of climate change in an Afrotropical centre of endemism. *Ecography* 36, 518–530.
- Pressey, R.L., Cowling, R.M., Rouget, M., 2003. Formulating conservation targets for biodiversity pattern and process in the Cape Floristic Region, South Africa. *Biol. Conserv.* 112, 99–127.
- Robinson, R.A., Green, R.E., Baillie, S.R., Peach, W.J., Thompson, D.L., 2004. Demographic mechanisms of the population decline of the song thrush *Turdus philomelos* in Britain. *J. Anim. Ecol.* 73, 670–682.
- Rondinini, C., Di Marco, M., Chiozza, F., Santulli, G., Baisero, D., Visconti, P., Hoffmann, M., Schipper, J., Stuart, S.N., Tognelli, M.F., Amori, G., Falucci, A., Maiorano, L., Boitani, L., 2011. Global habitat suitability models of terrestrial mammals. *Royal Soc. Philos. Trans. Biol. Sci.* 366, 2633–2641.
- Rowland, E.L., Davison, J.E., Graumlich, L.J., 2011. Approaches to evaluating climate change impacts on species: a guide to initiating the adaptation planning process. *Environ. Manage.* 47, 322–337.
- Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Biodiversity – global biodiversity scenarios for the year 2100. *Science* 287, 1770–1774.
- Schloss, C.A., Nunez, T.A., Lawler, J.J., 2012. Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *Proc. Natl. Acad. Sci. U.S.A.* 109, 8606–8611.
- Secretariat of the CBD, 2010. *Global Biodiversity Outlook 3*, Montréal.
- Seo, C., Thorne, J.H., Hannah, L., Thuiller, W., 2009. Scale effects in species distribution models: implications for conservation planning under climate change. *Biol. Lett.* 5, 39–43.
- Sinclair, S.J., Newell, G.R., White, M.D., 2010. How useful are species distribution models for managing biodiversity under future climates? *Ecol. Soc.*, 15.
- Sinervo, B., Mendez-de-la-Cruz, F., Miles, D.B., Heulin, B., Bastiaans, E., Villagrán-Santa Cruz, M., Lara-Resendiz, R., Martínez-Mendez, N., Lucía Calderón-Espinosa, M., Nelsi Meza-Lazaró, R., Gadsden, H., Javier Avila, L., Morando, M., De la Riva, I.J., Victoriano Sepulveda, P., Duarte Rocha, C.F., Irbarguengoytia, N., Aguilar Puntriano, C., Massot, M., Lepetz, V., Oksanen, T.A., Chapple, D.G., Bauer, A.M., Branch, W.R., Clobert, J., Sites Jr., J.W., 2010. Erosion of lizard diversity by climate change and altered thermal niches. *Science* 328, 894–899.
- Smith, R.J., Di Minin, E., Linke, S., Segan, D.B., Possingham, H.P., 2010. An approach for ensuring minimum protected area size in systematic conservation planning. *Biol. Conserv.* 143, 2525–2531.
- Summers, D.M., Bryan, B.A., Crossman, N.D., Meyer, A.S., 2012. Species vulnerability to climate change: impacts on spatial conservation priorities and species representation (vol 18, pg 2335, 2012). *Glob. Change Biol.* 18, 3268–3268.
- Tabor, K., Williams, J.W., 2010. Globally downscaled climate projections for assessing the conservation impacts of climate change. *Ecol. Appl.* 20, 554–565.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L., Williams, S.E., 2004. Extinction risk from climate change. *Nature* 427, 145–148.

- Thomas, C.D., Hill, J.K., Anderson, B.J., Bailey, S., Beale, C.M., Bradbury, R.B., Bulman, C.R., Crick, H.Q.P., Eigenbrod, F., Griffiths, H.M., Kunin, W.E., Oliver, T.H., Walmsley, C.A., Watts, K., Worsfold, N.T., Yardley, T., 2011. A framework for assessing threats and benefits to species responding to climate change. *Methods Ecol. Evol.* 2, 125–142.
- Thuiller, W., Lavorel, S., Araujo, M.B., Sykes, M.T., Prentice, I.C., 2005. Climate change threats to plant diversity in Europe. *Proc. Natl. Acad. Sci. USA* 102, 8245–8250.
- U.S. Environmental Protection Agency (EPA), 2009. A framework for categorizing the relative vulnerability of threatened and endangered species to climate change. National Center for Environmental Assessment, Washington, DC; EPA/600/R-09/011. Available from the National Technical Information Service, Springfield, VA, and <<http://www.epa.gov/ncea>>.
- Visser, M.E., Both, C., 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proc. Royal Soc. B* 272, 2561–2569.
- Wiens, J.A., Bachelet, D., 2010. Matching the multiple scales of conservation with the multiple scales of climate change. *Conserv. Biol.* 24, 51–62.
- Wiens, J.A., Stralberg, D., Jongsomjit, D., Howell, C.A., Snyder, M.A., 2009. Niches, models, and climate change: assessing the assumptions and uncertainties. *Proc. Natl. Acad. Sci. USA* 106, 19729–19736.
- Williams, S.E., Shoo, L.P., Isaac, J.L., Hoffmann, A.A., Langham, G., 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biol.* 6, 2621–2626.
- Williams, J.N., Seo, C., Thorne, J., Nelson, J.K., Erwin, S., O'Brien, J.M., Schwartz, M.W., 2009. Using species distribution models to predict new occurrences for rare plants. *Divers. Distrib.* 15, 565–576.
- Willis, S.G., Hill, J.K., Thomas, C.D., Roy, D.B., Fox, R., Blakeley, D.S., Huntley, B., 2009a. Assisted colonization in a changing climate: a test-study using two UK butterflies. *Conserv. Lett.* 2, 45–51.
- Willis, S.G., Thomas, C.D., Hill, J.K., Collingham, Y.C., Telfer, M.G., Fox, R., Huntley, B., 2009b. Dynamic distribution modelling: predicting the present from the past. *Ecography* 32, 5–12.
- WWF, 2012. Living Planet Report. WWF International, Gland, Switzerland.
- Young, B., Byers, E., Gravuer, K., Hall, K., Hammerson, G., Redder, A., 2011. Guidelines for Using the NatureServe Climate Change Vulnerability Index. Release 2.1. April 2011 <https://connect.natureserve.org/sites/default/files/documents/Guidelines_NatureServeClimateChangeVulnerabilityIndex_r2.1_Apr2011.pdf>.