Diversity and Distributions, (Diversity Distrib.) (2015) **21**, 1101–1111

Diversity and Distributions A Journal of Conservation Biogeography

BIODIVERSITY RESEARCH

Considering the impact of climate change on human communities significantly alters the outcome of species and site-based vulnerability assessments

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ABSTRACT

Aim Human activities are largely responsible for the processes that threaten biodiversity, yet potential changes in human behaviour as a response to climate change are ignored in most species and site-based vulnerability assessments (VAs). Here we assess how incorporation of the potential impact of climate change on humans alters our view of vulnerability when using well-established site and species VA methodologies.

Location Southern Africa.

Methods Our baseline was two published studies that used accepted VA methodologies aimed at examining the direct impacts of climate changes on species and sites. The first identified potential shifts in the distributions of 164 restricted-range avian species, the second forecasted species turnover in 331 Important Bird and Biodiversity Areas (IBAs). We used a published spatially explicit assessment of potential climate change impacts on people to evaluate which species and sites overlap with human populations most likely to be impacted. By doing this, we were able to assess how the integration of potential climate impacts on human populations changes our perception of which species and sites are most vulnerable to climate change.

Results We found no correlation between species and sites most likely to be impacted directly by climate change and those where the potential response of human populations could drive major indirect impacts. The relative vulnerability of individual species and sites shifted when potential impacts of climate change on human communities were considered, with more than one-fifth of species and one-tenth of sites moving from ‘low’ to ‘high’ risk.

Main conclusions Standard VA methodologies that fail to consider how people are likely to respond to climate change will result in systematically biased assessments. This may lead to the implementation of inappropriate management actions, and a failure to address those species or sites that may be uniquely, or additionally, imperilled by the impacts of human responses to climate change.

Keywords

Adaptation planning, climate change, conservation planning, human response, indirect impact, site vulnerability, species vulnerability, vulnerability assessment.

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DOI: 10.1111/ddi.12355
http://wileyonlinelibrary.com/journal/ddi

INTRODUCTION

The impact of climate change on global biodiversity is likely to be substantial (Thomas *et al.*, 2004; McClean *et al.*, 2005; Maclean & Wilson, 2011; Garcia *et al.*, 2012). Globally, anthropogenic climate change has already led to higher temperatures, altered rainfall regimes, and more frequent extreme weather and climatic events such as droughts, floods and heatwaves (Seneviratne *et al.*, 2012; IPCC, 2014). The proximate impacts of these physical changes on biodiversity can be defined as the direct impacts of climate change and are being reported with increasing frequency. Shifting or shrinking species ranges across the globe (Parmesan & Yohe, 2003; Ponce-Reyes *et al.*, 2012), changes in phenology leading to reduced fitness (Lane *et al.*, 2012), mass coral bleaching events (Hughes *et al.*, 2003) and complex changes in species assemblages (Gregory *et al.*, 2009) are just some of the impacts being reported.

As the dominant biotic and abiotic conditions that drive species presence and abundance are reshaped by climate change, human populations that occupy and are in many cases dependent upon the ecosystems that surround them are also adapting to the changing climatic conditions (Berrang-Ford *et al.*, 2011). There is now considerable evidence of humans responding to contemporary anthropogenic climate change, including through alteration of agricultural regimes (Howden *et al.*, 2007; Liu *et al.*, 2008), shifting fishing grounds (Pinsky & Fogarty, 2012), population migration (Feng *et al.*, 2010; Marchiori *et al.*, 2012; Bohra-Mishra *et al.*, 2014), changing transport routes (Prowse *et al.*, 2009) and preparation for natural disaster relief (Grantham *et al.*, 2011). The impacts from both the planned adaptation actions of human communities (e.g. coastal defence in response to sea-level rise and increased severe weather, Defeo *et al.*, 2009) and unplanned coping responses (e.g. increasing use of water resources in national parks by pastoralists during droughts, Ogutu *et al.*, 2009) are now thought to be impacting many species and ecosystems (Paterson, 2008; Turner *et al.*, 2010; Chapman *et al.*, 2014). Impacts on conservation targets (e.g. species, sites) that result from changes in human behaviour in response to climate change are increasingly referred to as the ‘indirect impacts’ of climate change (Chapman *et al.*, 2014) and we follow this convention.

The scientific community has responded to the challenge climate change poses for conservation in a significant way, with a large volume of literature applying different methodological approaches that primarily focus on understanding what current and future climate change is likely to mean for biodiversity and conservation in general (Akçakaya *et al.*, 2014; Chapman *et al.*, 2014; Pacifici *et al.*, 2015). For species vulnerability assessments (VAs), the most commonly used methods are correlative approaches that first relate the observed geographic range of a species to current climate, then use the resulting model, in conjunction with spatially explicit future climate projections, to produce estimates of the size and location of potentially climate-suitable areas for the species in the future (e.g. Thuiller *et al.*, 2005; Willis *et al.*, 2008; Carvalho *et al.*, 2010; Forero-Medina *et al.*, 2011). These models have the advantage of being spatially explicit and easily adaptable to a wide range of taxa at various spatial scales. Correlative models are also regularly used to assess forecasted changes in species composition in site-based climate VAs (Araújo *et al.*, 2004; Hannah *et al.*, 2007; Hole *et al.*, 2009, 2011). By assessing changes in species composition, the assessments provide an estimate of how the existing biotic character of a site might be altered by climate change.

Despite recent advances in these (and other) methodologies for assessing the vulnerability of species to climate change, a potentially serious shortcoming is that they are focused only on the ‘direct’ impacts (e.g. range shifts in response to altered temperature or precipitation regimes) of climate change on species and ecosystems (Chapman *et al.*, 2014; Pacifici *et al.*, 2015). The failure to consider the impacts of climate change on local human populations, and their likely responses, is a significant oversight, potentially resulting in systematically biased assessments of which species and sites are most vulnerable to climate change (Dawson *et al.*, 2011; Bellard *et al.*, 2012; Watson & Segan, 2013).

Here, we examine how integrating the potential impacts of climate change on people alters the outcome of traditional conservation VAs. We use data from two previously published studies that examined the direct impacts of climate change on species (Hannah *et al.*, 2013) and sites (Hole *et al.*, 2009) in southern Africa. These case studies represent two common treatments of climate change in the conservation literature: (i) those that consider the direct impacts of climate change on a set of species (Lawler *et al.*, 2009; Carvalho *et al.*, 2010) and (ii) those that consider the direct impacts of climate change on sites of conservation concern (Hannah *et al.*, 2007; Hole *et al.*, 2011; Monzón *et al.*, 2011). We first examine the vulnerability of these conservation targets as assessed against only the direct impacts of climate change. We then use a spatially explicit assessment of potential climate change-driven impacts on human communities in southern Africa (Midgley *et al.*, 2011) to identify species and sites likely to be affected by indirect impacts. We use this integrated understanding of the potential direct and indirect impacts of climate change to re-evaluate the exposure of species and sites to climate change-driven impacts and discuss the implications for conservation management.

METHODS

Impact of climate change on human populations

Spatially, explicit information on the likely impacts of climate change on human populations was sourced from an assessment conducted for the Regional Climate Change Programme for southern Africa (Midgley *et al.*, 2011). Midgley *et al.* (2011) considered a suite of 51 indicators to map three dimensions of vulnerability in 2050: exposure (i.e. the magnitude of projected climatic change), sensitivity (i.e. the extent to which the population is likely to be impacted by those changes) and adaptive capacity (i.e. potential to successfully respond or take advantage of changes) of human populations to climate change. Exposure was assessed with 16 indicators (e.g. drought recurrence interval, change in crop suitability and population growth), sensitivity with 16 indicators (e.g. water stress, crowding on agricultural land, soil degradation) and adaptive capacity with 19 indicators (e.g. health, economic wealth, governance). For each dimension, expert opinion was used to develop weightings for the contribution of each indicator to the dimension. The weighted indicators were then summed to derive independent layers for each dimension of vulnerability. Individual dimensions were then selectively integrated to assess both 'impact' (defined as the combination of exposure and sensitivity) and 'vulnerability' (defined as the combination of exposure, sensitivity and the inverse of adaptive capacity) of human populations. We used 'impact' as a proxy for the human response (and thus indirect impact on biodiversity) because it integrates likely exposure and sensitivity (Glick *et al.*, 2011; Midgley *et al.*, 2011) and is therefore the most appropriate proxy for where people will be most affected and thus pressed to respond. We believed Midgley *et al.*'s (2011) vulnerability measure was not appropriate for our purposes, because we are interested primarily in identifying where people are likely to respond, not where they are most likely to need assistance in responding. We argue that impacted human populations with high adaptive capacity are as likely to adapt in ways that may negatively impact biodiversity (e.g. using hard-engineered approaches such as dams to address climate change-driven water shortages), as impacted populations with low adaptive capacity (e.g. who may rely on increased abstraction of water from rivers or wetlands). We note that it is impossible to predict specific, spatially explicit human adaptation responses from the Midgley *et al.* (2011) dataset, and we discuss this issue in the Discussion.

Midgley *et al.* (2011) forecasted relative impact on human populations at one km^2 resolution, on a scale that ranged from 4 to 53, where higher values indicate greater impact in 2050 (Midgley *et al.*, 2011). We rescaled the grid cell impact scores to range between 0 and 100, by subtracting the minimum score from each, dividing by the range and then multiplying by 100:

$$S_p = (P_s - \min P)/(\max P - \min P) \times 100 \qquad (1)$$

After rescaling, mean grid cell impact score was 65, and the distribution exhibited a slight negative skew. The rescaled measure of the impact of climate change on people was used as a proxy for indirect impacts on biodiversity or the relative likelihood of people responding, in some manner, to climate change.

Species assessment

Species with specialized habitat requirements and species that occupy narrow geographic ranges have frequently been suggested to be more vulnerable to climate change (Sekercioglu *et al.*, 2008; Foden *et al.*, 2013). Restricted-range terrestrial bird species are defined as avian species that occupy a range $< 50{,}000$ km^2 (Long *et al.*, 1996). Hannah *et al.* (2013) assessed the vulnerability of 1263 restricted-range terrestrial bird species to climate change-induced range loss. They built species distribution models (SDMs) in Maxent for each species using six climate variables and cross-referenced the current ranges against predictions from six other SDMs. Forecasts for the distribution of each species in 2050 and 2080 were developed using downscaled projections of future climatic conditions from five general circulation models. We limited our assessment to the 164 extant species with ranges that coincide with the human populations assessed by Midgley *et al.* (2011).

Following what has become standard practice in the assessment of species vulnerability to the direct impact of climate change, we calculated the proportion of each species' current range that is projected to remain climatically suitable in 2050 (Carvalho *et al.*, 2010; Visconti *et al.*, 2011). Forecasted loss for each species was then calculated as one minus the proportion of the species current range that is forecasted to remain climatically suitable. This is a conservative approach to assessing potential direct impacts as it assumes that species are unable to colonize new areas. The no-colonization assumption is likely to be appropriate for assessing the future range of restricted-range species whose distribution is likely limited more by non-climate factors (Schwartz, 2012), but we report on different scenarios that explore alternative assumptions about species' ability to colonize new areas in Appendix S1 in Supporting information. To assess potential indirect impacts on species, we calculated the mean human impact score within the portion of the species' range forecasted to remain climatically suitable in 2050.

Site-based assessment

Important Bird and Biodiversity Areas (IBAs) are sites of international significance for the conservation of the world's birds and other biodiversity, whose identification is coordinated by the BirdLife International Partnership (BirdLife International, 2014a). Hole *et al.* (2009) assessed the direct impact of climate change on 803 IBAs in sub-Saharan Africa by evaluating expected changes in species composition due to climate change in each IBA. Presence–absence data for 1608 species across sub-Saharan Africa were used to develop SDMs for each species, for the present-day climate and for two future time periods (2055 and 2085), using future climate projections from three GCMs. Modelled presence or absence of each species in each IBA, for each time period, was determined by projecting each species range using individual stratified climates generated for each IBA (to avoid using a single 'average' climate for each IBA) (Hole *et al.*, 2009). 'Species turnover' within each IBA was then calculated as the sum of all species expected to gain or lose suitable climate within each IBA, divided by the total number of species projected to occur in the IBA in the present-day and in 2055 (or 2085). Here, we used forecasted species turnover in 2055 to represent the magnitude of avian community disruption expected in each IBA, as a result of the direct impacts of climate change. We calculated potential indirect impacts on each IBA as the mean human impact score within the IBA inclusive of a 50 km^2 buffer around the IBA. A 50 km^2 buffer around the IBA was used to account for impacts from human activity that may originate from spatially proximate populations (McDonald *et al.*, 2009).

Integrating direct and human (indirect) impacts

To identify species and sites where their vulnerability, based on the direct impacts of climate change, changed after additional consideration of indirect impacts, we classified their relative exposure to direct and indirect impacts on a simple ordinal scale (low, medium or high). Species and IBAs with scores one standard deviation above or below the mean were defined as high and low, respectively, while all scores within one standard deviation of the mean were classified as medium. The sensitivity of our findings to the choice of classification criterion was explored by repeating the classification with two alternative definitions of low and high impact (See Appendix S2).

RESULTS

Species assessment

There was a weak negative correlation between forecasted species range loss and species exposure to potentially impacted human populations (Pearson's $r(162) = -0.42$, $P < 0.01$). Seven species were forecasted to lose their entire range to the direct impact of climate change, while nine species were not forecasted to experience any range loss. We identified 28 species with a mean forecasted range loss of 88.5% (SD = 11.4) as high direct impact species and 32 species with a mean forecasted range loss of 3.2% (SD = 3.1) as low direct impact species. When we overlaid the likely impact of climate change on human populations with species ranges, we identified a further 21 species as high indirect impact species (mean = 77.1, SD = 3.5) (Fig. 1). We found no difference in mean indirect impact in the ranges of species classified as high and low direct impact (Welch's *t*-test, $t(35.6) = -1.2$, $P = 0.26$), suggesting that the lack of correlation between forecasted direct and indirect impact on species holds true even at the ends of the distribution.

We identified seven low direct impact species (25.0% of low direct impact species and 4.2% of all birds) and five high direct impact species (17.9% of high direct impact species and 3.1% of all birds) that are found in areas where human populations are likely to be highly impacted by climate change (Fig. 2). A sensitivity analysis showed that the species most likely be overlooked by a VA focused only on direct impacts was robust to alternative assumptions around species' ability to colonize new areas (Appendix S1).

Site-based assessment: Important Bird and Biodiversity Areas

There was no correlation between forecasted species turnover and exposure to human populations potentially impacted by climate change across IBAs (Pearson's $r(329) = -0.08$, $P = 0.16$). We identified 48 (14.5%) IBAs as low direct

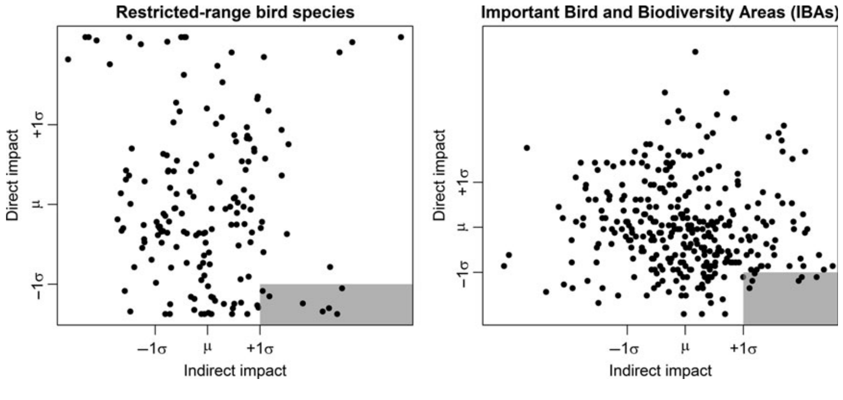
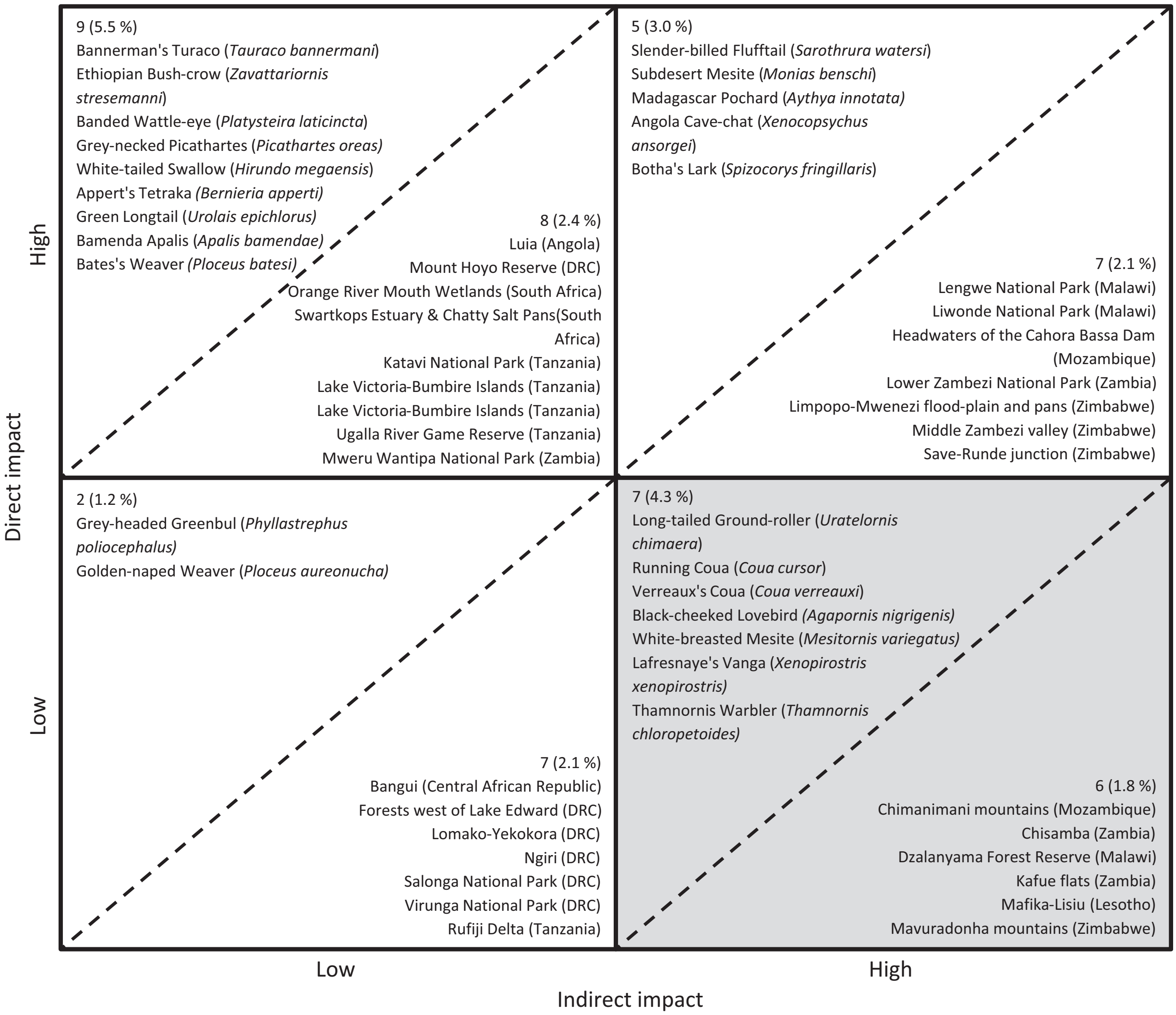


Figure 1 Relationship between the potential direct and indirect impacts of climate change on species and sites. Direct impact for bird species was defined as the extent to which the species current range is forecasted to remain climatically suitable in 2050 (Hannah *et al.*, 2013) with higher values indicating greater loss of climatically suitable range. Direct impact on IBA sites was defined as forecasted species turnover in response to climate changes by 2055 (Hole *et al.*, 2009). Potential indirect impact was assessed as the mean forecasted impact of climate change on human populations in 2050 (as assessed by Midgley *et al.*, 2011) within the species range or within the IBA inclusive of a 50 km^2 buffer. The grey area in the lower right corner highlights the species and sites most likely to be overlooked if we relied only on standard vulnerability assessment methodologies that only consider the direct impacts of climate change and corresponds to the species and sites in Figure 2. Species and sites identified as most likely to be overlooked are those with low direct impact scores (at least one standard deviation below the mean) and high indirect impact scores (at least one standard deviation above the mean).



9 (5.5 %)
Bannerman's Turaco (*Tauraco bannermani*)
Ethiopian Bush-crow (*Zavattariornis stresemanni*)
Banded Wattle-eye (*Platysteira laticincta*)
Grey-necked Picathartes (*Picathartes oreas)*
White-tailed Swallow (*Hirundo megaensis*)
Appert's Tetraka *(Bernieria apperti)*
Green Longtail (*Urolais epichlorus)*
Bamenda Apalis (*Apalis bamendae)*
Bates's Weaver *(Ploceus batesi)*

8 (2.4 %)
Luia (Angola)
Mount Hoyo Reserve (DRC)
Orange River Mouth Wetlands (South Africa)
Swartkops Estuary & Chatty Salt Pans(South Africa)
Katavi National Park (Tanzania)
Lake Victoria-Bumbire Islands (Tanzania)
Lake Victoria-Bumbire Islands (Tanzania)
Ugalla River Game Reserve (Tanzania)
Mweru Wantipa National Park (Zambia)

5 (3.0 %)
Slender-billed Flufftail (*Sarothrura watersi*)
Subdesert Mesite (*Monias benschi*)
Madagascar Pochard (*Aythya innotata)*
Angola Cave-chat (*Xenocopsychus ansorgei*)
Botha's Lark (*Spizocorys fringillaris*)

7 (2.1 %)
Lengwe National Park (Malawi)
Liwonde National Park (Malawi)
Headwaters of the Cahora Bassa Dam (Mozambique)
Lower Zambezi National Park (Zambia)
Limpopo-Mwenezi flood-plain and pans (Zimbabwe)
Middle Zambezi valley (Zimbabwe)
Save-Runde junction (Zimbabwe)

2 (1.2 %)
Grey-headed Greenbul (*Phyllastrephus poliocephalus)*
Golden-naped Weaver (*Ploceus aureonucha)*

7 (2.1 %)
Bangui (Central African Republic)
Forests west of Lake Edward (DRC)
Lomako-Yekokora (DRC)
Ngiri (DRC)
Salonga National Park (DRC)
Virunga National Park (DRC)
Rufiji Delta (Tanzania)

7 (4.3 %)
Long-tailed Ground-roller (*Uratelornis chimaera*)
Running Coua (*Coua cursor*)
Verreaux's Coua (*Coua verreauxi*)
Black-cheeked Lovebird *(Agapornis nigrigenis)*
White-breasted Mesite (*Mesitornis variegatus)*
Lafresnaye's Vanga (*Xenopirostris xenopirostris)*
Thamnornis Warbler (*Thamnornis chloropetoides)*

6 (1.8 %)
Chimanimani mountains (Mozambique)
Chisamba (Zambia)
Dzalanyama Forest Reserve (Malawi)
Kafue flats (Zambia)
Mafika-Lisiu (Lesotho)
Mavuradonha mountains (Zimbabwe)

Figure 2 Bird species and IBA sites identified as most (and least) likely to be affected by the direct and indirect impacts of climate change. Bird species appear above the diagonal line, and IBA sites are included below the diagonal. Direct impact for bird species was defined as forecasted loss of climatically suitability range in 2050 (Hannah *et al.*, 2013). Direct impact for IBA sites was defined as the forecasted species turnover by 2055 (Hole *et al.*, 2009). Potential indirect impact was defined as mean forecasted impact of climate change on human populations in 2050 (as quantified by Midgley *et al.*, 2011) within the species range or within the IBA inclusive of a 50 km^2 buffer. High and low impacts were defined, respectively, as impact scores one standard deviation above or below the mean. The figure identifies seven (4.3%) species and six (1.8%) sites that would be completely missed by vulnerability assessments focused only on direct impacts (highlighted in grey). Figure 3 provides some examples of these species and their locations, and Fig. 4 provides the locations of these sites.

impact sites with a mean forecasted species turnover of 7.6% (SD = 3.0) and 55 (16.6%) IBAs as high direct impact sites with a mean forecasted turnover of 44.3% (SD = 6.8). A further 50 (15.1%) IBAs were identified as high indirect impact sites with a mean forecasted human impact score of 79.2 (SD = 2.8), and 49 (14.1%) IBAs were identified as low indirect impact sites with a mean human impact score of 56.7 (SD = 3.5). We found no difference in mean forecasted human impact between sites classified as high and low direct impact (Welch's *t*-test, $t(99.4) = 0.57$, $P = 0.57$).

We identified six low direct impact IBAs (1.8% of all IBAs) that are in areas where the human populations are likely to highly impacted by climate change (high indirect impact) (Figs 2 & 4). These sites are most likely to be overlooked by VAs focused only on the direct impact of climate change. We identified an additional seven high direct impact IBAs (2.1% of all IBAs) where highly impacted human populations are likely to further complicate conservation management (Fig. 2).

DISCUSSION

While there are a number of published papers that have identified the need to incorporate the human response to climate change in conservation planning (Turner *et al.*, 2010; Watson & Segan, 2013; Watson, 2014), this is the first

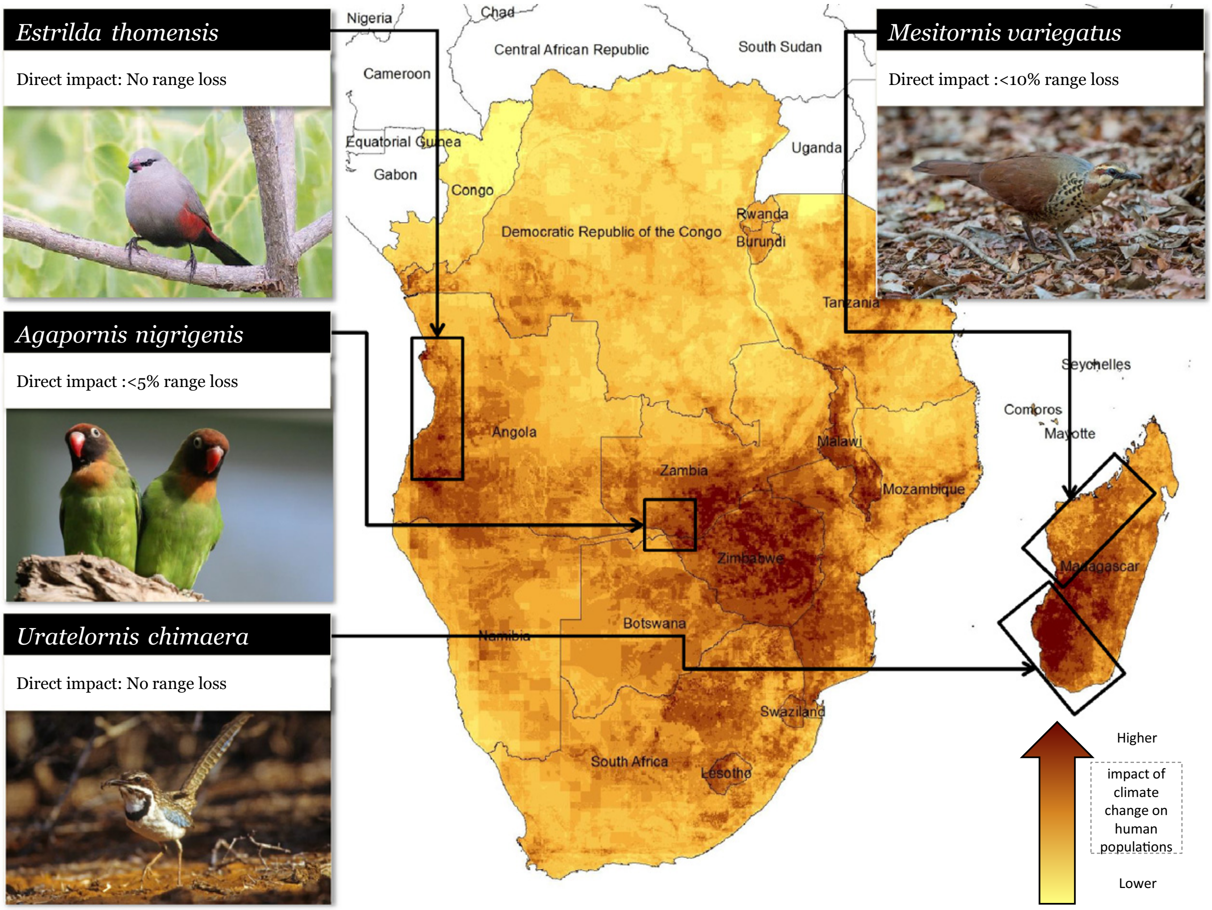


Figure 3 Examples of species likely to be overlooked by climate change assessments focused only on direct impacts (see Figure 2 and Figure 1). The existing range of the Cinderella waxbill (Estrilda thomensis) (Photo credit: Johann Grobbelaar), black-cheeked lovebird *(Agapornis nigrigenis)* (Photo credit: Nathan Rupert), long-tailed ground-roller (*Uratelornis chimaera*) (Photo credit: Stuart Butchart) and White-breasted Mesite (Mesitornis variegatus) (Photo credit: Wim de Groot) is forecasted to remain climatically suitable; however, the human populations within each species range are likely to be highly impacted by climate change. Direct impact was defined as the extent to which the species current range is forecasted to remain climatically suitable in 2050 (Hannah *et al.*, 2013). Potential indirect impact on each species was defined as the mean impact of climate change on human populations forecasted in 2050 (as assessed by Midgley *et al.*, 2011) within the species range.

assessment to our knowledge that formally integrates an assessment of the potential impact of climate change on human populations into either a species or site-based VA. We found no positive correlation – for sites or species – between those forecasted to be most affected by the direct impacts of climate change and those where proximate human populations were most likely to be impacted. If this finding holds true for conservation targets in other regions, then climate change conservation priorities identified without respect to the human response should be re-examined.

When individual targets were considered, only five (3.0%) species and seven (2.1%) sites identified as highly vulnerable to the direct impacts of climate change were spatially congruent to human populations that were also likely to be highly impacted by climate change. Conversely, we found that seven species (4.3%) and six sites (1.8%) identified as least likely to be affected by the direct impacts of climate change are found in areas where human populations are likely to be highly impacted by climate change. This is likely to be a conservative estimate, given that the potentially negative impacts on biodiversity arising from people's adaptation responses will vary significantly depending on the nature of the response. Human populations are critical actors in socio-ecological systems and are the primary force driving processes that currently threaten most species (Hilton-Taylor *et al.*, 2009). Hence, the incorporation of spatially explicit information that addresses the likelihood of people responding to climate change provides essential information for the robust assessment of vulnerability of biodiversity.

Vulnerability assessments are used by governments, conservation organizations and industry to inform planning and allocate resources (Rodrigues *et al.*, 2006; Hoffmann *et al.*, 2008; Joseph *et al.*, 2009; Bernazzani *et al.*, 2012; Brown *et al.*, 2013). It is critical that such processes are informed by the best available science about what impacts are likely to occur. We demonstrate that including information on where

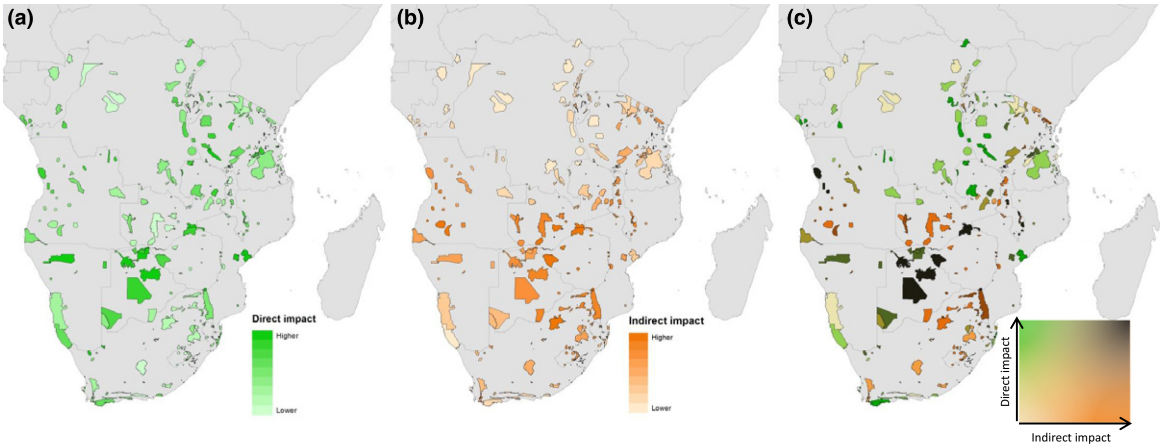


Figure 4 Forecasted direct and indirect impacts of climate change on IBAs in southern Africa. (a) Projected turnover in species composition by 2055 due to forecasted climate change (direct impact) as assessed by Hole *et al.* (2009). Darker colours indicate higher levels of turnover. (b) Potential indirect impact defined as the mean impact of climate change on human populations as assessed by Midgley *et al.* (2011) inside the IBA (inclusive of a 50 km^2 buffer). Darker colours indicate higher levels of impact on human populations. (c) Overlay of the projected direct and indirect impact of climate change on IBA sites in southern Africa. Orange colours indicate IBAs that are most likely to be overlooked by vulnerability assessments that focus only on the direct impacts of climate change. Species turnover in these sites as a result of direct climate changes is forecasted to be low, but the potential responses of highly impacted local human communities may drive indirect impacts on sites.

human populations are likely to respond to climate change alters our understanding of which species are most likely to be impacted by climate change and how. For example, we found that the long-tailed ground-roller (*Uratelornis chimaera)*, a member of a Madagascan endemic family that is highly vulnerable to habitat loss (BirdLife International, 2014b), is not forecasted to lose any of its range due to the direct impact of climate change. When the impact of climate change on people was assessed, the human communities in its range had the third highest impact score of any species evaluated. Forecasted reductions in agricultural productivity in surrounding areas due to climate change (Hannah *et al.*, 2013) could be devastating for the local Malagasy population and intensify pressure to clear additional land to maintain current yields, resulting in direct habitat loss for the species. It is highly likely that the long-tailed ground-roller will become increasingly vulnerable as people respond to changing climatic conditions, even if the species current range remains climatically suitable. To ensure the persistence of the long-tailed ground-roller, efforts are needed to address human vulnerability with appropriate responses that do not impact the species and its habitat.

The species- and site-based VAs we use as case studies quantified the direct impacts of climate change through projected shifts in species ranges simulated by SDMs. Despite their prevalence in VAs in the conservation literature, there are considerable uncertainties and limitations associated with their application to conservation decision-making (Schwartz, 2012). In addition to shifting range, species' potential responses to climate change may also take the form of behavioural changes or altered phenologies for example (Bellard *et al.*, 2012). Trait-based VAs that utilize species-specific traits, including dispersal ability, habitat requirements and dependence on environmental cues or other species (Foden *et al.*, 2013; Garcia *et al.*, 2014; Pacifici *et al.*, 2015), offer an alternative to niche modelling that may better reflect species ability to engage in adaptive responses other than range shifts. However, these VAs almost invariably overlook potential human responses as well, and the seven bird species we identified as most likely to be overlooked (projected low direct, high indirect impacts) would also have been overlooked (identified as less vulnerable to climate change) if we had used a trait-based assessment of direct impacts (Foden *et al.*, 2013).

Our results show that prioritization of sites or site-based management strategies based only on the forecasted movement of species in response to the direct impacts of climate change (e.g. Araújo *et al.*, 2004; Hannah *et al.*, 2007; Hole *et al.*, 2011) also need to be revisited to reflect potential human responses. Understanding how the direct impacts of climate change shape species composition is necessary but not sufficient to assess site vulnerability or identify appropriate management actions or prioritize resources between sites. Human populations in and around these areas are already responding to climate change, and conservation action must account for these changes. In the Kafue flats IBA in Zambia, for example, the direct impact of climate change on native bird species is expected to be relatively low (species turnover less than 10%), but the local human population is likely to be highly impacted (Fig. 2). The site is a seasonally flooded wetland, with a flow regime regulated by hydropower dams. Although in principle the flow regime mimics natural inundation regimes, fears around water shortages have meant that those agreements have not always been fully implemented (BirdLife International, 2013). The expected increase in the frequency and intensity of extreme climatic events such as droughts (Seneviratne *et al.*, 2012; IPCC, 2014) may increase pressure on managers to deviate away from natural flow regimes and towards one that primarily serves to satisfy the water demands of local agriculture. Such a deviation could have substantial negative impacts on species-dependent on natural flow regimes. Climate change clearly poses a risk to the site, but that risk is only apparent when the potential response of human populations is incorporated into the VA. The situation is far from unique: half of African IBAs are currently threatened by habitat loss to agriculture (BirdLife International, 2004), and climate change is likely to significantly alter agricultural suitability across Africa (Adeloye, 2010), potentially completely reshaping the spatial pattern and nature of the threat.

The primary contribution of our work is to illustrate the importance of including information on where human populations are likely to respond to climate change, in order to improve our understanding of the vulnerability of any form of conservation target. This permits the identification of conservation targets previously thought to be at relatively low risk to climate change that now warrant further attention because they are potentially imperilled by the responses of human populations. This exposes a potentially major gap in our ability to assess impacts, namely that knowing where people are more likely to respond tells us little about what their response(s) will be. The IPCC groups potential human adaptation responses into three non-mutually exclusive categories: ‘structural/physical’, which are discrete undertakings with identifiable products (e.g. seawall construction, vaccine programmes and alternative crop types); ‘social’, which includes responses such as promoting education or household preparedness for disasters; and ‘institutional’, which include policy options such as taxes, economic incentives and land use zoning (IPCC, 2014). The type of adaptation response an ‘actor’ (e.g. individual, household, community or government entity) engages in will result in potentially dramatically different impacts on local biodiversity. Limited evidence to date suggests that when people engage in adaptive actions, they are usually motivated by climate change in concert with other factors (e.g. economic conditions or recent natural disasters) that drive the enabling conditions for change (Berrang-Ford *et al.*, 2011; Ford *et al.*, 2011). This makes defining how people are going to respond, in any given area, for any given climate change impact, enormously challenging, and represents a core avenue for future research and evidence synthesis. The challenge is then to connect specific human adaptation responses to individual or aggregate impacts on biodiversity, in a spatially explicit framework. While broad ‘rules-of-thumb’ may be applicable for some responses, reality will invariably be more complex.

Human responses that benefit some species may result in negative impacts on other species; for example, it has been shown that dam construction can benefit some waterfowl by creating new habitat, while negatively impacting species for which the dam presents a migration barrier and those reliant on the current nutrient dynamics or downstream inundation patterns (McAllister *et al.*, 2001). The impacts of some human responses on biodiversity may also be counter-intuitive. The potential for people to migrate in response to climate change has received significant media attention despite recognition that the decision to migrate is complex and may be driven by a suite of non-climatic factors (Black *et al.*, 2011). Lower human population density is generally considered beneficial for biodiversity (Sanderson *et al.*, 2002), so it may seem logical to conclude that as people move away from a portion of the landscape the prospects for local biodiversity will also improve. However, in the northern Amazon, researchers have observed that as people vacate rural areas the ability to control fires decreases dramatically, resulting in increased fire risk (Schwartz *et al.*, 2015). In accounting for the human response, it is essential to consider the complex feedback loops between that response and other stressors that impact biodiversity. Again, research and synthesis is urgently needed to better understand the implications of the wide range of potential human adaptation responses on biodiversity.

Finally, it is also important to recognize that some human responses, such as efforts to reduce atmospheric carbon through mechanisms like REDD+, can provide significant benefits to biodiversity by conserving or restoring habitat (Turner *et al.*, 2010). Similarly, leveraging the services provided by natural ecosystems to reduce human vulnerability to climate change (ecosystem-based adaptation) is an emerging approach in climate change adaptation that offers the promise of improving outcomes for both people and biodiversity (Jones *et al.*, 2012). For example, protection and restoration of coastal ecosystems (e.g. reefs, tidal marshes, mangroves) is often a viable alternative to conventionally engineered coastal defences (e.g. seawalls, dykes) as a means of enhancing flood protection for coastal human populations. In addition to providing a potentially lower cost and more sustainable option for coastal defence, ecosystem protection and restoration can provide additional benefits to fisheries and coastal species (Temmerman *et al.*, 2013; Jupiter *et al.*, 2014). Identifying these potential ‘win-wins’ will be critical to efficiently allocate resources to meet the needs of biodiversity and people. Failure to consider the full scope of the interaction in the socio-ecological system may result in a lost opportunity to identify areas and adaptation solutions that benefit both biodiversity and people (McClanahan *et al.*, 2008).

In the interdependent and complex socio-ecological systems in which biodiversity conservation increasingly takes place, the identification of appropriate and sustainable management responses for supporting the persistence of conservation targets under climate change requires considering all the pathways, both direct and indirect, by which climate change may impact the system. Failure to account for the aggregate impacts of climate change may result in two outcomes that impede success of global conservation efforts. First, the species, sites and ecosystems that are most vulnerable to climate change may be being overlooked because of a failure to consider the impacts that most imperil them. Second, conservation actions planned without consideration of the full suite of impacts are likely to be near-sighted, suboptimal and may not succeed over the long term.

ACKNOWLEDGEMENTS

We thank N. Bailey, K. Mutu, W. Foden and J. Carr for comments and discussion on earlier ideas and versions of this manuscript. We thank four anonymous referees for constructive feedback on a previous version of the manuscript. We are also grateful to S. Midgley, R. Davies, L. Hannah, S. Willis and M. Ikegami for providing data used in the analysis. This work was made possible by the generous support of the American people through the United States Agency for International Development (USAID) under the terms of Cooperative Agreement No. RLA-A-00-07-00043-00. The contents are the responsibility of the authors and do not necessarily reflect the views of USAID or the United States Government.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Alternative assumptions on species dispersal capacity.

Appendix S2 Sensitivity of vulnerability classification to definition impact.

BIOSKETCH

The authors are consortium of leading scientists from different global conservation NGOs and universities who have come together and pooled data to work on climate change adaptation across Africa.

Editor: David Richardson