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BIODIVERSITY RESEARCH

Assessing species vulnerability to climate and land use change: the case of the Swiss breeding birds

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ABSTRACT

Aim Climate warming and land use change represent a major challenge for both species and conservation managers. Temporally and spatially explicit projections of the future distribution of species have been extensively developed to support decision-making in conservation. The aim of this study was to move beyond the simple projections of likely impacts of global change to identify the most vulnerable species. We suggest an original vulnerability index that integrates estimations of projected range change and different proxies of species resilience in a quantitative way. The proposed index is generally applicable, completely quantitative, and it allows ranking species so as to prioritize conservation actions.

Location We illustrate the applicability of the vulnerability index using breeding birds in Switzerland as an example of conservation target.

Methods The vulnerability index relies on five indicators quantifying different aspects of the projected change in distributional area, the reservoirs available for the species and their recent population trend. Species distribution was modelled using three different techniques (GAM, MARS and BRT) and then projected for 2050 and 2100 according to two different IPCC scenarios of climate change coupled with two regional land use scenarios to represent different magnitudes of the stressors and the range of possible outcomes.

Results According to the different contributions of the base indicators, different patterns of vulnerability can be distinguished. In Switzerland, breeding birds inhabiting coniferous woodlands, alpine habitats and wetlands have significantly higher vulnerability to climate and land use change than species in other habitats.

Main conclusions The proposed vulnerability index represents an early warning system as it identifies species that are currently not threatened, but are very likely to become so. As such, it complements the assessment of risk of species' extinction based on the Red List and on their international importance.

Keywords

Breeding birds, climate and land use change, conservation priorities, early warning system, Switzerland, vulnerability index.

INTRODUCTION

Global change is forcing species to either 'move, adapt or die' (Carvalho *et al.*, 2010; Maggini *et al.*, 2011). The consequences of a warming climate and the intensification of human activities on landscapes represent important challenges for conservation as they have already led to extinctions of species, and high extinction rates are predicted for

the future (Parmesan & Yohe, 2003; Jetz *et al.*, 2007). Land use change has certainly been the major driver of biodiversity loss in the past century due to its immediate impact on the habitats of many species, but climate change will probably become as important in the next decades in some landscapes (Sekercioglu *et al.*, 2008; Dawson *et al.*, 2011). Hence, it is urgent to develop not only temporally and spatially explicit projections on how these environmental changes might affect the abundance and distribution of species in the future; it is also necessary to identify the most vulnerable species so as to efficiently inform authorities and managers about oncoming conservation priorities.

Vulnerability is a term applied to a variety of systems and defined in various ways across disciplines. All definitions agree that four main elements are necessary to define vulnerability: the vulnerable entity, the attribute of concern (e.g. existence, health, biodiversity), an identified hazard/stressor (e.g. climate change) and a temporal reference for the vulnerability assessment (Füssel, 2007). It is also widely accepted that the vulnerability of a system is a function of its sensitivity to stressors and adaptive capacity to change (McCarthy *et al.*, 2001), and its resilience, that is the ability of a system to recover from perturbations or to shift to another stable state (Folke, 2006).

Several attempts have been made to propose a generally applicable conceptual framework for assessing vulnerability across disciplines (e.g. Füssel, 2007). Often, this requires the assessment of vulnerability of single species which make up an ecosystem and its services to humans (Midgley *et al.*, 2002; Sekercioglu *et al.*, 2004), and to identify regions where species might specifically become at risk (Beaumont *et al.*, 2011). A significant step forward in species vulnerability assessment was the proposition of a unified framework by Williams *et al.* (2008) which theoretically identifies the different components of vulnerability and their inter-relations. However, it remains an open question how these theoretical components can be translated into identifiable and measurable units applicable to practice.

The aim of this paper was to propose an objective and quantitative index assessing the vulnerability of species exposed to global change which assists in the prioritization of conservation actions. Several examples exist of vulnerability assessed by expert knowledge based on traits that are known to foster species vulnerability (e.g. habitat specialization, low dispersal ability; e.g. Foden *et al.*, 2008; Isaac *et al.*, 2009) or by expert judgment of the likely impact of changes in different climate variables on species (e.g. Fuentes & Cinner, 2010). We acknowledge the value of such expert approaches, especially when a rapid assessment is needed. Yet, qualitative assessment cannot account for the magnitude of impact caused by stressors. Here, we propose a quantitative vulnerability index based on the impact of two stressors, climate and land use change. We used two spatially explicit scenarios to represent different magnitudes of the stressors and to assess their impact on species distribution using species distribution models (Elith & Leathwick, 2009). We also incorporated indicators of resilience and a proxy of species-specific factors.

One strength of our work is that likely future distribution ranges are projected according to changes not only in climate but also in land use. This decreases the inaccuracy of the projections because land use allows reshaping the potential distribution defined by the climatic envelope to something closer to the actual area of occupancy of the species. Our vulnerability index was developed for the entire breeding avifauna of Switzerland, but the approach can be applied to any species of concern in any area provided that certain basic data are available, thus resulting in indices that are comparable between species of different taxonomic groups.

METHODS

Concepts underlying the Vulnerability index

According to the framework proposed by Williams *et al.* (2008), species vulnerability depends both on the exposure to external factors, such as climate and habitat change, and on intrinsic factors that determine the species' sensitivity to those changes. Sensitivity is thought to depend mainly on ecological traits, physiological tolerance and genetic diversity of the species, characteristics that will finally determine its adaptive capacity and resilience (Williams *et al.*, 2008). Although terms such as exposure, sensitivity, adaptive capacity and resilience are intuitively clear concepts, their translation into measurable entities for an operational definition of vulnerability is difficult. To pragmatically and quantitatively assess the vulnerability of Swiss breeding birds, we estimated on the one hand the impact of the projected climate and land use changes (exposure) on the distribution of the species (result of species' sensitivity) within Switzerland assuming a behavioural plasticity allowing them to shift their distribution with unlimited dispersal capability (adaptive capacity). This is a fair assumption for this case study, but for other taxonomic groups in other areas, it may be advisable to also consider a scenario of 'no dispersal' to represent the range of possible outcomes according to different dispersal abilities. On the other hand, we estimated different proxies of resilience: the likely recruitment capacity within Switzerland and from surrounding countries, as well as the recent population trend of each species in Switzerland, which serves as a proxy for the many species-specific factors not accounted for (e.g. ecological traits, factors acting outside the Swiss breeding range during migration and wintering).

The definition of the vulnerability index (VI) and its base indicators

We defined our vulnerability index using five indicators expressing three operational aspects of vulnerability: the projected change in the distribution, the reservoirs for the species and the population trend. Each indicator was defined as

to vary between 0 (no contribution to vulnerability) and 1 (maximal contribution).

Two indicators (I_{AO} and $I_{Overlap}$) capture the change in the species' distribution within Switzerland.

$$I_{AO} = AO/(AO + AO') \quad (1)$$

I_{AO} relates the current (AO, km^2) and the future area of occupancy (AO', km^2) of the species and measures the relative amount of change that is projected as a consequence of the selected global change scenario. In our case, all species considered were already breeding within Switzerland, so that AO is always greater than zero.

$$I_{Overlap} = 1 - Overlap/AO \quad (2)$$

$I_{Overlap}$ accounts for the relative overlap between the current and future area of occupancy of the species (overlap measured in km^2). The indicator expresses that the more the current and future areas are disconnected, the more difficult it is to colonize the future area.

The following two indicators (I_{ReCH} and I_{ReEU}) represent the reservoirs of a species.

$$I_{ReCH} = 1 - (AO'/41301) \quad (3)$$

I_{ReCH} expresses the size of the future area of occupancy of the species within Switzerland (41301 km^2 being the total area of Switzerland and thus the maximum content of the Swiss reservoir). Species with restricted ranges are indeed more prone to extinction and more vulnerable to climate change (Ohlemüller et al., 2008).

The resilience of Swiss populations will likely depend on the geographic position of Switzerland with respect to the European distribution of the species. If Switzerland is located at the southern margin of the European distribution, the recruitment possibilities from neighbouring European countries will be limited as the range will generally shift towards northeast following climate warming (Huntley et al., 2007). To account for recruitment from surrounding countries, the European reservoir was defined as the 72 grid cells (squares of 50 × 50 km) of the Atlas of European breeding birds (Hagemeijer & Blair, 1997) surrounding Switzerland, that is approximately a 100–km buffer around the Swiss territory (see Appendix S2 in Supporting Information). The 100–km buffer is supposed to cover the potential range shift of species populations over the study period (roughly 90 years) and is coherent with the findings of Brommer et al. (2012) concerning past latitudinal range shifts for bird species breeding in central Europe which is of 1.1–1.3 km/year poleward.

$$I_{ReEU} = 1 - (N/72) \quad (4)$$

I_{ReEU} refers to the proportion of the 72 grid cells occupied by a given species. For 2100, the content of the reservoir was defined by the predictions of the Climatic Atlas of European breeding birds (Huntley et al., 2007). For 2050, it was calculated as the mean between the current (according to the Atlas of European Breeding Birds; Hagemeijer & Blair, 1997) and the projected 2100 content.

Fine-scale environmental relationships, intrinsic characteristics and population dynamics of a species are difficult to capture and quantify for a large number of species. As a proxy of these species-specific aspects, we used the population trend over the past 19 years.

$$I_{Trend} = 1 - (Slope_{sp} - Slope_{min})/(Slope_{max} - Slope_{min}) \quad (5)$$

I_{Trend} relates the slope of the population trend of a given species ($Slope_{sp}$) to the minimum ($Slope_{min}$) and maximum slope ($Slope_{max}$) observed among all Swiss breeding birds. For common species, Swiss population trends over the period 1990–2008 were calculated using a GLM with a Poisson distribution within the programme TRIM, whereas for rare species, trends were estimated with site occupancy models (Pannekoek & van Strien, 1998; Zbinden et al., 2005; Kéry et al., 2010). We used I_{Trend} as a proxy for species-specific characteristics for the following reasons. The first four indicators assess the vulnerability of a species on the basis of the projected changes in distribution and reservoirs. However, projections only represent the potential for range expansion/retraction on the basis of climate and land use change, and the actual range change will in reality also depend on current population viability and dynamics, information that we approximated by population trend. Moreover, by including population trend, we indirectly incorporate the life history traits of species, more detailed aspects of the ecological and demographic relationship of the species with its environment (e.g. abundance of food, nest site availability, availability of micro-habitats, competition with other species) and events occurring outside Switzerland during migration and the non-breeding season. Indeed, several traits (habitat specialization, annual fecundity, diet, natal dispersal) are known to be correlated with the population trend (Jiguet et al., 2007; Van Turnhout et al., 2010). We did not extrapolate population trends into the future because of the large uncertainty involved and because population size is deemed to be correlated with range size (O'Grady et al., 2004) which is already captured by the indicator I_{AO}.

These five indicators were averaged to obtain a final vulnerability index varying between 0 (species not vulnerable) and 1 (species highly vulnerable). The final vulnerability index (VI) is calculated as the mean of the three operational aspects of vulnerability (Fig. 1): the change in the distribution within the study area (represented by I_{AO} and $I_{Overlap}$); the reservoirs for the species (represented by I_{ReCH} and I_{ReEU}); and the population trend (represented by I_{Trend}):

$$VI = [(I_{AO} + I_{Overlap})/2 + (I_{ReCH} + I_{ReEU})/2 + I_{Trend}]/3 \quad (6)$$
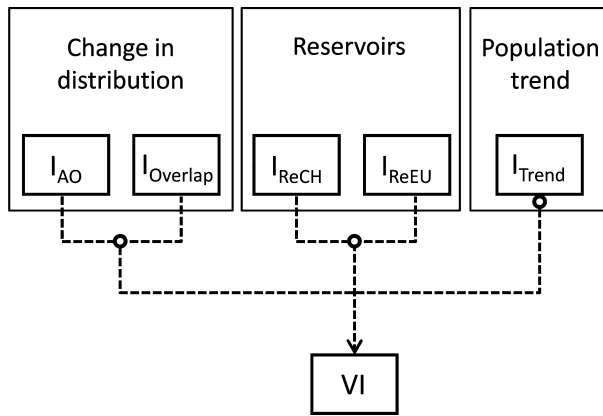
Figure 1 The contribution of the three operational aspects of vulnerability to the final vulnerability index (VI): (i) the change in the distribution within Switzerland (represented by the mean of two indicators: the estimated relative change in the projected area of occupancy of the species under future climate and land use change, I_{AO}; the proportion of overlap of the future relative to the current area of occupancy, $I_{Overlap}$); (ii) the reservoirs for the species (represented by the mean of two indicators: extent of the future area of occupancy within Switzerland, i.e. the Swiss reservoir for the species, I_{ReCH}; the relative position of Switzerland with respect to the European range of the species, i.e. the content of the 'European' reservoir defined around Switzerland, I_{ReEU}); (iii) the population trend (represented by one indicator: the trend of the Swiss populations over the last 19 years, I_{Trend}). The final VI is the mean of the three operational aspects of vulnerability, that is $[(I_{AO} + I_{Overlap})/2 + (I_{ReCH} + I_{ReEU})/2 + I_{Trend}]/3$.

Scenarios of global change

Projections of species distribution into the future are highly dependent on the greenhouse gas emissions scenario considered (Dormann *et al.*, 2008). We considered two scenarios to represent the lower and upper bounds of anthropogenic interference with the climate system. The distribution of each species was modelled using three different techniques of species distribution modelling (GAM, MARS and BRT) and then projected for the 21st century according to the IPCC scenarios A1FI and B2 (IPCC SRES, 2000) regionalized for Switzerland using the downscaling method described in Engler *et al.* (2011). The details concerning the modelling of the species distributions and the projections are provided in Appendix S1 of Supporting Information: the document describes the approach we used in our case study, but should not be considered as a protocol. Researchers should design their modelling following the best practice and latest developments in the field and according to the organism under study. Climatic scenarios were combined with land use scenarios specifically developed for Switzerland (Bolliger *et al.*, 2007): the 'liberalization' scenario (LIB) was coupled with the A1FI scenario and assumes that the agricultural markets are no longer subsidized with the consequence that farming in the mountains is largely abandoned. The 'lowered

agricultural production' scenario (LAP) is coupled with the IPPC scenario B2 and assumes large-scale adoption of agri-environmental schemes that foster sustainable land use (for details, see Appendix S1).

For each combined scenario (i.e. A1FI × LIB and B2 × LAP), projections were performed for two time frames: 2050 and 2100. A vulnerability index was calculated for each combined scenario and time frame, and designated according to the name of the climatic scenario (A1, B2) and the last two digits of the assessed year (2050, 2100): $VI_{a1.50}$, $VI_{b2.50}$, $VI_{a1.00}$ and $VI_{b2.00}$. These indices express the vulnerability of the species to the projected changes in climate and land use in the future. However, some species are already today more vulnerable than others when considering their current geographical range or population trend (i.e. without considering future developments). A reference vulnerability index (VI_{ref}) referring to this initial level of vulnerability for the species was thus calculated on the basis of the present-time values of the indicators I_{ReCH}, I_{ReEU} and I_{Trend}, and by assuming $AO' = AO$ (as a consequence, I_{AO} was set to 0.5 and $I_{Overlap}$ to 0).

RESULTS

A total of 173 species were initially considered for the analysis, but four of them, namely the Mew Gull (*Larus canus*), White-spotted Bluethroat (*Luscinia svecica cyanecula*), Pallid Swift (*Apus pallidus*) and Grey Partridge (*Perdix perdix*), have very localized distributions within Switzerland and only few observations within the databases which prevent proper modelling. These species were therefore discarded from the analysis as were three supplementary species, namely the Collared Flycatcher (*Ficedula albicollis*), the Hooded Crow (*Corvus corone cornix*) and the Italian Sparrow (*Passer hispaniolensis italiae*), for which information on population trend was not available.

We calculated vulnerability indices for 166 current regular breeding bird species of Switzerland under the two combined scenarios of climate and land use change A1FI × LIB (extreme) and B2 × LAP (moderate), and for the two time frames 2050 and 2100, as well as the reference index (denoted $VI_{a1.50}$, $VI_{a1.00}$, $VI_{b2.50}$, $VI_{b2.00}$ and VI_{ref}; see Appendix S3).

Apart from very few exceptions, model goodness-of-fit of the underlying species distribution models showed to be good to excellent (Table S1, Appendix S1). AUC values indeed ranged between 0.8 and 1 for 92.9 % of the GAM and MARS models, and for 98.1% of the BRT models, of which more than half were actually between 0.9 and 1. Models also proved to be stable as AUC values remained good to excellent after cross-validation (10-fold): 91% of GAM, 91.6 % of MARS and 92.9 % of BRT models showed cross-validated AUC values between 0.8 and 1.

Below, we identify the habitats of the most vulnerable species and their different vulnerability patterns, we compare the vulnerability index with the categorization of the Red List of threatened breeding birds of Switzerland, we combine the

notion of vulnerability and international importance to assess conservation priorities and we compare the vulnerability indices for different time frames. This is a subset of possible analyses, and we invite readers to use the indices available in Appendix S3 for further analyses.

Vulnerability of species inhabiting different habitats

The vulnerability indices of the Swiss breeding bird species for the B2 × LAP scenario and the 2100 time frame differed across habitat types (Fig. 2). Species of coniferous woodlands (mean $VI_{b2.00} = 0.57$), alpine habitats (0.51) and wetlands (0.47) have significantly higher vulnerability indices than species inhabiting farmland (mean $VI_{b2.00} = 0.39$), dry habitats (0.35), broadleaved woodlands (0.34), settlements (0.32) or mixed habitats (0.35; Wilcoxon signed-rank test $P < 0.05$ in all cases). A similar pattern among habitats is obtained when considering the vulnerability indices for the extreme scenario A1FI × LIB for 2100. In addition, $VI_{a1.00}$ values are
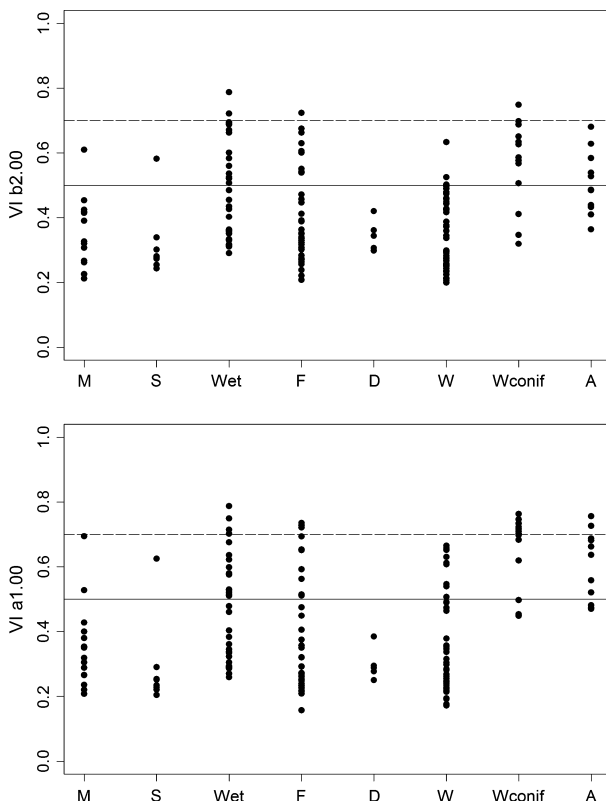
significantly higher than $VI_{b2.00}$ values for birds inhabiting coniferous woodlands ($P < 0.001$ according to a paired Wilcoxon signed-rank test) and alpine habitats ($P < 0.01$).

Patterns of vulnerability

The vulnerability index of a species is determined by the different contributions of the five base indicators. Five typical patterns of vulnerability can be distinguished (example species given in Fig. 3) which represent the extremes of a continuum. The first pattern (Fig. 3a) is dominated by high indicator values related to changes in the area of occupancy (I_{AO}, $I_{Overlap}$, I_{ReCH}) which increase with increasing time frame and from the moderate to the extreme scenario. The second pattern (Fig. 3b), characterized by low Swiss and European reservoirs (I_{ReCH}, I_{ReEU}), is typical for species that are presently rare within the Swiss territory, but are projected to spread under future conditions (decreasing I_{ReCH} over time), such as Mediterranean species. The vulnerability of these species is also determined by the European reservoir (I_{ReEU}) that is partially empty. The third pattern (Fig. 3c) is mainly determined by a negative trend of the Swiss population. The fourth pattern is that of non-vulnerable, widespread species (Fig. 3d), for which the values of all indicators are low. The fifth pattern characterizes highly vulnerable species (Fig. 3e), in particular boreal or alpine species which are projected to lose a large part or even all of their breeding area in Switzerland and in the neighbouring countries. The vulnerability of species characterized by this pattern becomes a real threat as soon as the populations start to decrease.

Vulnerability, threat of extinction and international importance

Red Lists categorize species according to their risk of extinction (IUCN, 2010). Although part of the criteria, future threats of climate and land use change are seldom integrated when assessing threat status for Red Lists because the necessary information is often lacking, coarse or on a short term. As a consequence, the ranking of species according to the vulnerability index developed here does not correlate with the classification in the Swiss Red List (Keller *et al.*, 2010) (Fig. 4). This shows that information on long-term future threats can make a great difference when assessing threat status for Red Lists. The two classifications match for species such as Eurasian Curlew *Numenius arquata*, or Northern Lapwing *Vanellus vanellus* characterized by both a high vulnerability and a high extinction risk (CR, critically endangered). However, the two classifications disagree for species that are threatened with extinction in Switzerland today, but are not projected to be highly vulnerable in the future (Woodchat Shrike *Lanius senator* and Ortolan Bunting *Emberiza hortulana*). These species prefer habitats that are presently rare in Switzerland, but they are expected to benefit from the projected increase in temperature. More interesting

Figure 2 Vulnerability indices for species inhabiting different types of habitats: M, mixed habitats; S, settlements; Wet, wetlands; F, farmland; D, dry habitats and cliffs; W, lowland woodland; Wconif, coniferous woodland; A, alpine habitats. Upper panel: $VI_{b2.00}$ vulnerability index calculated according to the combined scenario B2 × LAP for 2100. Lower panel: $VI_{a1.00}$ vulnerability index calculated according to the combined scenario A1FI × LIB for 2100. Solid line: vulnerability index = 0.5. Dashed line: vulnerability index = 0.7 (to be used as visual landmark).
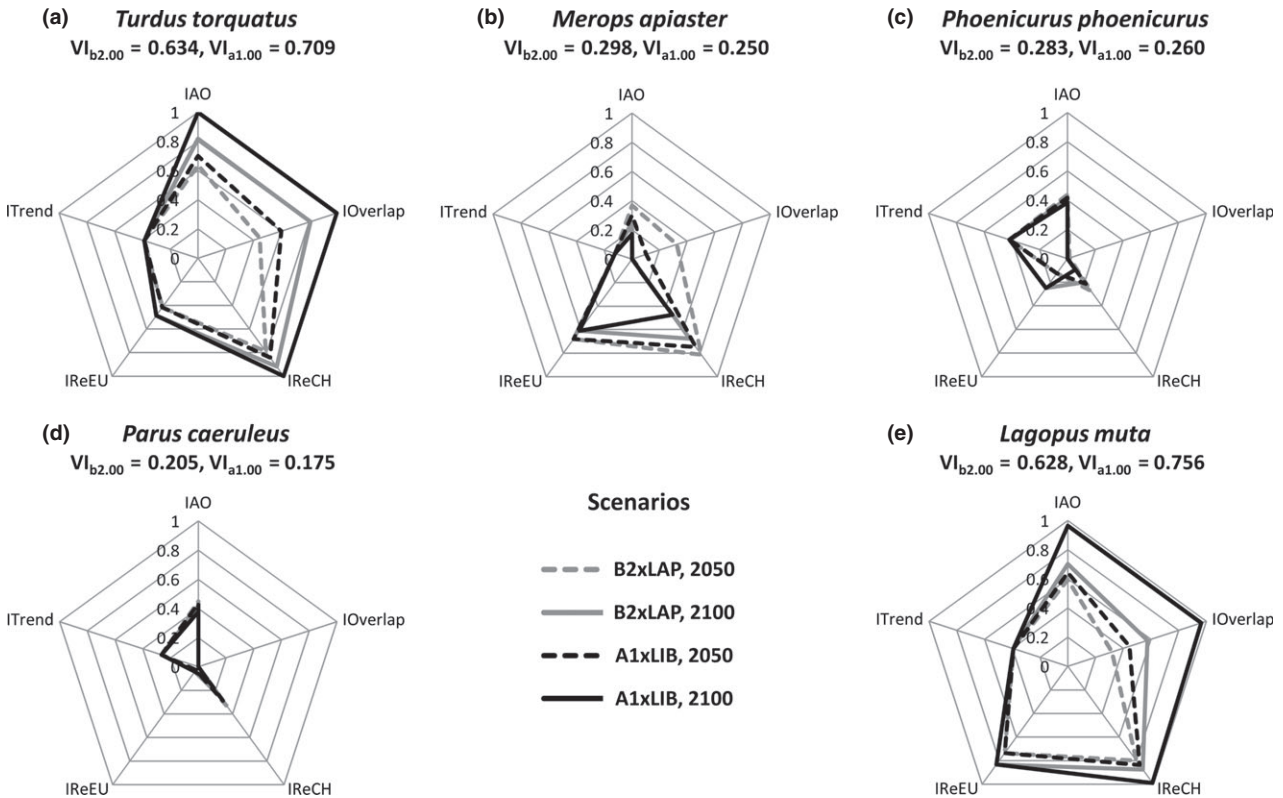
Figure 3 Spider graphs of example species representing different patterns of vulnerability with their associated contributions from the five base indicators: I_{AO}, indicator related to the change in the area of occupancy; $I_{Overlap}$, indicator accounting for the overlap between present and future area of occupancy; I_{ReCH}, indicator informing about the range of the species within Switzerland; I_{ReEU}, indicator informing about the relative position of Switzerland with respect to the European distribution of the species; I_{Trend}, indicator related to the trend of the Swiss populations. Vulnerability index: $VI_{a1.00}$ = vulnerability index calculated for 2100 according to the A1FI × LIB scenario; $VI_{b2.00}$ = vulnerability index calculated for 2100 according to the B2 × LAP scenario.

is a particular group of species that is of least concern (LC) today according to the Swiss Red List, but characterized by high vulnerability (VI > 0.7) (Fig. 4). This group includes species that are presently not threatened but will very likely become so in the future. These are species with a distribution centred in northern or north-eastern Europe (Spotted Nutcracker *Nucifraga caryocatactes*, Boreal Owl *Aegolius funereus*, Eurasian Pygmy Owl *Glaucidium passerinum*, Eurasian Three-toed Woodpecker *Picoides tridactylus*), or in the Alps (Citril Finch *Serinus citrinella*, White-winged Snowfinch *Montifringilla nivalis*).

As a complement to the risk of extinction determined by Red Lists, the international importance of a regional (national) population for the global survival of a species is used as a criterion to establish conservation priorities (Keller & Bollmann, 2004; Schmeller *et al.*, 2008). There is a substantial group of species which are vulnerable (VI > 0.7), and for which Switzerland holds internationally important populations (Fig. 5). These species, once again, inhabit alpine habitats or coniferous forests and are characterized by a distribution centred in the Alps (e.g. *Montifringilla nivalis*, *Serinus citrinella*), in Northern Europe (e.g. *Glaucidium passerinum*, *Aegolius funereus*, *Picoides tridactylus*) or in both regions (e.g. *Lagopus muta*, *Turdus torquatus*).

Vulnerability under different scenarios and time frames

When we compare the vulnerability index for 2100 with the reference index, it appears that $VI_{b2.00}$ and $VI_{a1.00}$ are higher than VI_{ref} for most species (Fig. 6). This indicates that climate and land use change increase the vulnerability of most Swiss breeding bird species, while in a minority of species, vulnerability decreases. Species with $VI_{a1.00} > VI_{ref}$ have their distribution centred in northern Europe and are thus near the southern margin of their distribution in Switzerland today. They are linked to subalpine coniferous and alpine habitats (e.g. Rock Ptarmigan *Lagopus muta*, Ring Ouzel *Turdus torquatus*, Boreal Owl *Aegolius funereus*, Eurasian Bullfinch *Pyrrhula pyrrhula*), and to farmland (Fieldfare *Turdus pilaris*, Whinchat *Saxicola rubetra*). Species with a $VI_{a1.00} < VI_{ref}$ are mainly of Mediterranean origin (e.g. European bee-eater *Merops apiaster*, Eurasian Hoopoe *Upupa epops*), species related to thermophile habitats (Rock Bunting *Emberiza cia*, Blue Rock Thrush *Monticola solitarius*), but also species linked to farmland (Western Yellow Wagtail *Motacilla flava*, Little Owl *Athene noctua*, Ortolan Bunting *Emberiza hortulana*).

Not surprisingly, the difference between VI_{ref} and the 2100 VI is generally larger for the extreme scenario (A1FI × LIB)
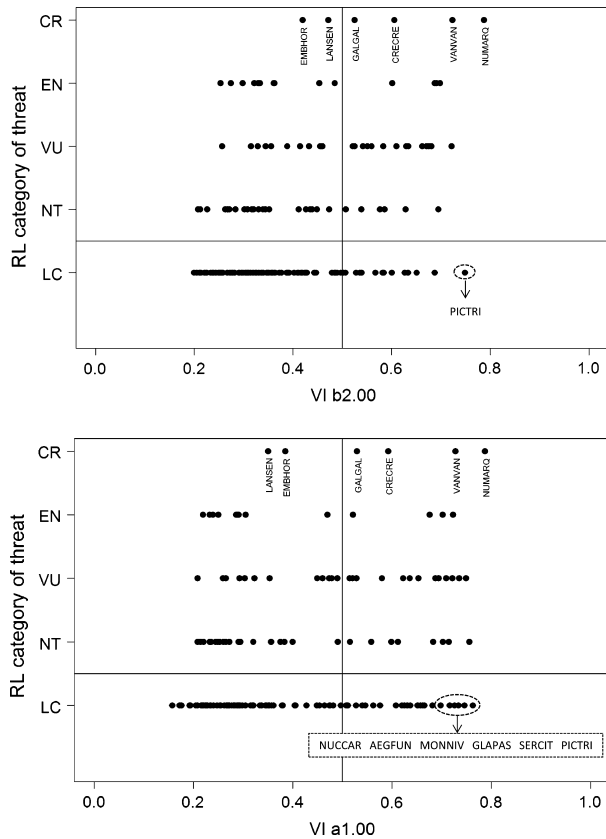
Figure 4 Vulnerability index and category of risk of extinction according to the Swiss Red List 2010 (Keller *et al.*, 2010) for the 166 assessed species (dots). VI$_{b2.00}$: vulnerability index calculated according to the combined scenario B2 × LAP for 2100. VI$_{a1.00}$: vulnerability index calculated according to the combined scenario A1FI × LIB for 2100. Red List categories: CR, critically endangered; EN, endangered; VU, vulnerable; NT, near threatened; LC, least concern. In each graph, the ellipse surrounds species that are of least concern (LC) in the Red List, but have a high vulnerability index (VI > 0.7). AEGFUN, *Aegolius funereus*; CRECRE, *Crex crex*; EMBHOR, *Emberiza hortulana*; GALGAL, *Gallinago gallinago*; GLAPAS, *Glaucidium passerinum*; LANSEN, *Lanius senator*; MONNIV, *Montifringilla nivalis*; NUCCAR, *Nucifraga caryocatactes*; NUMARQ, *Numenius arquata*; PICTRI, *Picoides tridactylus*; SERCIT, *Serinus citrinella*; VANVAN, *Vanellus vanellus*.

than for the moderate scenario (B2 × LAP), which indicates that the impacts of climate and land use change are stronger for the A1FI × LIB than for the B2 × LAP scenario. Under the moderate B2 scenario, wetland species are also among the highly vulnerable species (e.g. Savi's Warbler *Locustella luscinioides*, Spotted Crake *Porzana porzana*).

DISCUSSION

Advantages and limitations of the index

The species vulnerability index proposed here has several advantages over other approaches. We directly incorporated
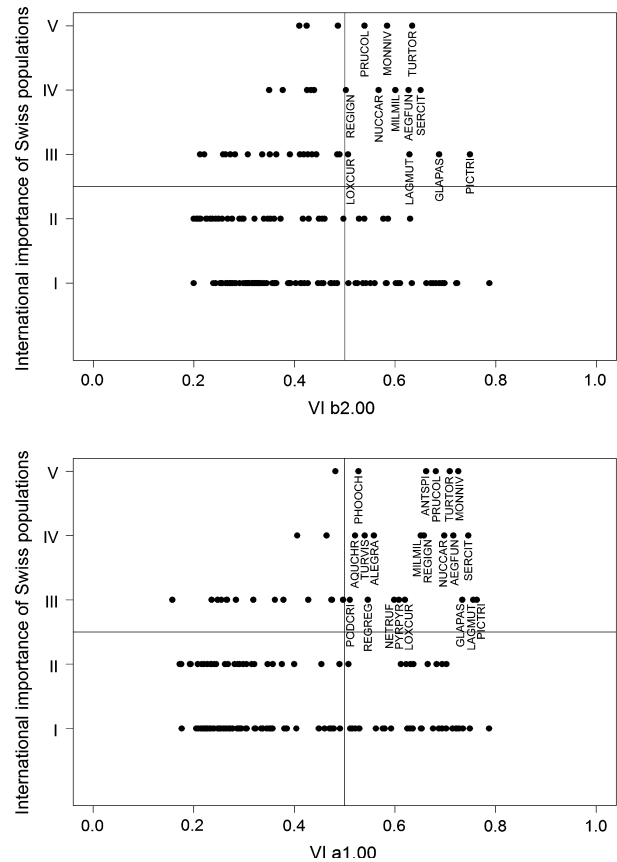
Figure 5 Vulnerability index and category of international importance of Swiss populations for the 166 assessed species (dots). VI$_{b2.00}$: vulnerability index calculated according to the combined scenario B2 × LAP for 2100. VI$_{a1.00}$: vulnerability index calculated according to the combined scenario A1FI × LIB for 2100. Classes of international responsibility established according to the percentage of the European population occurring in Switzerland (Keller & Bollmann, 2004): I = less than 0.7%, II = 0.7–1.4 %, III = 1.4–3.5%, VI = 3.5–7%, V = more than 7%. Categories III to V are considered to be of high international responsibility (Keller & Bollmann, 2004). AEGFUN, *Aegolius funereus*; ALEGRA, *Alectoris graeca*; ANTSPI, *Anthus spinoletta*; AQUCHR, *Aquila chrysaetos*; GLAPAS, *Glaucidium passerinum*; LAGMUT, *Lagopus muta*; LOXCUR, *Loxia curvirostra*; MILMIL, *Milvus milvus*; MONNIV, *Montifringilla nivalis*; NETRUF, *Netta rufina*; NUCCAR, *Nucifraga caryocatactes*; PHOOCH, *Phoenicurus ochruros*; PICTRI, *Picoides tridactylus*; PODCRI, *Podiceps cristatus*; PRUCOL, *Prunella collaris*; PYRPYR, *Pyrrhula pyrrhula*; REGIGN, *Regulus ignicapilla*; REGREG, *Regulus regulus*; SERCIT, *Serinus citrinella*; TURTOR, *Turdus torquatus*; TURVIS, *Turdus viscivorus*.

the impacts of new sources of threat such as climate and land use change by accounting for the distributional changes that are projected to occur under different scenarios of global change. Our vulnerability index accounts for the magnitude of the changes and, therefore, is fully quantitative and allows to rank species according to their vulnerability.

Figure 6 Comparison of the vulnerability index for the end of the century with the reference index. The line represents identity; black dots above the identity line correspond to species whose index is projected to increase and dots below the line to species whose index is projected to decrease over the 21st century. Upper panel: $VI_{b2.00}$ – vulnerability index calculated according to the combined scenario B2 × LAP for 2100. Lower panel: $VI_{a1.00}$ – vulnerability index calculated according to the combined scenario A1FI × LIB for 2100. The code of the Latin name is given only for the 10% of the species that have the greatest increase/decrease in the vulnerability index. ACRARU, *Acrocephalus arundinaceus*; AEGFUN, *Aegolius funereus*; APUMEL, *Apus melba*; ATHNOC, *Athene noctua*; BONBON, *Bonasa bonasia*; CAPEUR, *Caprimulgus europaeus*; EMBCIA, *Emberiza cia*; EMBCIR, *Emberiza cirlus*; EMBHOR, *Emberiza hortulana*; FICHYP, *Ficedula hypoleuca*; GLAPAS, *Glaucidium passerinum*; IXOMIN, *Ixobrychus minutus*; LAGMUT, *Lagopus muta*; LANSEN, *Lanius senator*; LARMIC, *Larus michahellis*; LOCLUS, *Locustella luscinioides*; LOXCUR, *Loxia curvirostra*; LUSMEG, *Luscinia megarhynchos*; LUSSVE, *Luscinia svecica*; MERAPI, *Merops apiaster*; MILMIL, *Milvus milvus*; MONSAX, *Monticola saxatilis*; MONSOL, *Monticola solitarius*; MOTFLA, *Motacilla flava*; NUCCAR, *Nucifraga caryocatactes*; NUMARQ, *Numenius arquata*; OTUSCO, *Otus scops*; PASDOM, *Passer domesticus*; PICTRI, *Picoides tridactylus*; PORPOR, *Porzana porzana*; PRUMOD, *Prunella modularis*; PYRPYR, *Pyrrhula pyrrhula*; REGIGN, *Regulus ignicapilla*; SAXRUB, *Saxicola rubetra*; SERCIT, *Serinus citrinella*; SYLBOR, *Sylvia borin*; SYLNIS, *Sylvia nisoria*; TETURO, *Tetrao urogallus*; TURPIL, *Turdus pilaris*; TURTOR, *Turdus torquatus*; UPUEPO, *Upupa epops*; VANVAN, *Vanellus vanellus*.

Life history traits and ecological factors are notoriously difficult to integrate in such an index and require a detailed knowledge about each species. In particular, we could not account for future changes in habitat quality, but most species will be affected by more specific habitat changes than those captured by the broad land use variables traditionally used in modelling exercises (Jetz *et al.*, 2007). We indirectly captured ecological and life history traits through the indicator I_{Trend}. Indeed, population trend correlates with many ecological and life history traits (Jiguet *et al.*, 2007; Van Turnhout *et al.*, 2010). Together with population size, trend is one of the most efficient predictors of demographic risk (O'Grady *et al.*, 2004) and thus indirectly informs on the resilience of the species. Other proxies of resilience could be considered instead or in combination with population trend, such as rates of historical population recoveries, measures of population variability around the smoothed trend, or modelled demographic rates that could be integrated directly into mechanistic models to obtain more realistic spatial predictions.

For the vulnerability index proposed here, we weighted the three operational aspects of vulnerability (change in distribution, reservoirs and population trend) equally. We gave I_{Trend} the same weight as for change in distribution and for reservoirs because even if projections predict an increase in the area of occupancy of a species, this will not happen if the current trend is negative and the population in strong decline. When changing the weights of the indicators, the individual ranking of the species will of course change, but the vulnerability indices are still highly correlated (correlation coefficients > 0.974; see Appendix S4).

The factors we used to estimate vulnerability, although relevant, only allow an approximation of total vulnerability. The index does not consider the possibility of a species to adapt to new conditions or to find micro-refugia that would allow persistence in the current range (Austin & Van Niel, 2011). This is a well-known limitation of species distribution modelling in which projections into the future are based on niche conservatism, and the existence of micro-refugia is often neglected because they can only be captured by fine-scale models (Zurell *et al.*, 2009). However, the ecological niche is deemed to be quite conservative (Peterson, 2011), and micro-refugia are mainly expected in the area of overlap between present and future distribution (Keppel *et al.*, 2011), an element that is taken into account by our index.

When predicting changes in the area of distribution, two counteracting problems need to be traded-off: the risk of overestimating a shrinkage in distribution because the distribution was calculated from only a part of the range (in this case Switzerland) and the risk of overestimating the area of distribution because of spatially coarse predictors (modelling is generally performed at a 50 km resolution at the European level) (Jetz *et al.*, 2008). For this study, we decided to work on a fine scale (1 km). This allowed us to include land use change data which are only available for Switzerland. We also think that estimating the future distribution from the

current distribution in Switzerland (and not Europe or the entire range of the species) is warranted, because Switzerland with its very high topographic diversity (resulting in many different climates from very wet to very dry and from very cold to very hot) captures almost all habitat types of Europe (except semi-deserts). Hence, we deem the risk of overestimating a shrinkage in distribution because the distribution was calculated from only a part of the range as small or non-existent for most species, and we consider the possibility of incorporating land use change projections (available for Switzerland at a fine resolution), a significant advantage.

Applicability of the index

The index is based on five simple and measurable indicators that require a relatively limited knowledge of the species' distribution and population trend. As such, this index can be calculated for species of various taxonomic groups within different areas of assessment. However, depending on the characteristics of the taxonomic group, the area and the availability of data, some modifications of the index may be required.

For example, vulnerability indices for a taxonomic group with very little dispersal ability will imply to consider a 'no dispersal' scenario while projecting the distribution into the future (i.e. the portion of the future favourable habitat that is outside the current area of occupancy of the species is filtered out). For species with intermediate dispersal abilities, a realistic dispersal scenario may be applied and the projections filtered according to the estimated distance that the species is able to cover by the time horizon of the projections.

In cases of limited knowledge about population trends, coarse categories of population change may be used instead (category -1 = declining; category 0 = stable; category 1 = increasing population). The corresponding indicator would then be defined as:

$$I_{PopChange} = 1 - (category - lower\ category)/(higher\ category - lower\ category)$$

(7)

giving an indicator value of 1 (maximal contribution to vulnerability) for a declining population, and a value of 0 (no contribution to vulnerability) for an increasing population.

Alternatively, this indicator could be replaced by an indicator of life history or demographic traits.

Significance of the vulnerability index

The five base indicators contribute differently to the vulnerability of a species and allow to identify four main types within a continuum (see Fig. 3): (1) well-established species which become vulnerable because of a projected shrinkage of the area of occupancy; (2) species of Mediterranean origin which are presently rare but predicted to become widespread in Switzerland in the future; (3) species whose vulnerability is mainly determined by the negative population trend; (4) species for which all the indicators, except I_{trend}, contribute to their vulnerability, that is mainly alpine and boreal species.

The indicators taken into account in our vulnerability index are analogous to those used to define the extinction risk of a species for the Red List according to IUCN criteria (IUCN, 2010), namely indicators concerning geographic range size, population size and population trend. However, our vulnerability index considers longer projections into the future than the three generations used for IUCN criteria and thus specifically points to species that will be most at risk in the future. The two classifications are thus complementary in the information they provide.

Indeed, our analysis identified an important group of species that are presently not considered as being at risk of extinction (category 'least concern' of the Swiss Red List) but are characterized by a high vulnerability index. Many of these are either alpine species or species with a distribution centred in N/NE Europe. With climate warming, both groups of species are predicted to shift their distribution to higher elevations (some are already doing so; Maggini et al., 2011), or to the NE (Huntley et al., 2007). This is expected to result in drastic reductions of their distribution area or even in their disappearance from Switzerland. The vulnerability index is thus very useful in raising awareness concerning species that are not currently threatened, but will likely become endangered in the future. Our vulnerability index, which indicates changes beyond the time frame used in Red List assessments, may thus be part of an early warning or alert system.

Like the Red List, our vulnerability index is not necessarily sufficient to determine species conservation priorities. Other factors (e.g. costs, logistics, chances of success, additional biological characteristics) should be taken into account (Miller et al., 2006). Conservation targets should be selected on the basis of irreplaceability, as is widely done within the framework of reserve selection approaches (Margules & Pressey, 2000). While there exists no endemic breeding bird in Switzerland, there are species for which Switzerland has a great international responsibility considering the high proportion of the European population concentrated on Swiss territory (Keller & Bollmann, 2004). The highly vulnerable species for which Switzerland also holds a high responsibility are, again, mainly species with a distribution centred in the Alps, Northern Europe or both.

Not surprisingly, the species that will benefit from a warming climate are mainly species of Mediterranean origin, adapted to dry habitats, which are projected to increase in Switzerland and its surroundings in the future. Some farmland species seem to benefit from the projected expansion of farmland under the A1FI × LIB scenario (Fig. 6). However, this result should be interpreted with caution as their distribution depends on the intensity of farming (which is not included in the models), rather than on the mere presence of farmland. Species projected to be most vulnerable are mainly alpine and boreal species that may lose a significant part, or

all, of their habitat by 2100. This holds especially for the extreme scenario (A1FI × LIB) with its higher increase in temperature. Among the highly vulnerable species are also wetland species. These are unlikely to find new wetlands to colonize, given their rarity, their propensity to dry out as a consequence of warmer temperatures, altered precipitation regime and inadequate management and human pressure towards more intense land use.

Conservation priorities and perspectives

In summary, the proposed vulnerability index complements the assessment of extinction risk based on the Red List and on international importance. In particular, the vulnerability index points at species which are currently not threatened, but are likely to become so under various climate change scenarios. Their persistence in Switzerland is at risk over the next 50–100 years.

In the case of Switzerland, conservation measures to reduce the effects of climate change on breeding birds should focus on alpine and boreal species (in particular those which cannot retreat towards northern Europe) and to wetland species. Their remaining habitats should be preserved and exempted from human disturbance. Wetlands need to be specifically conserved, and their water balance managed in appropriate ways to counteract the likely increase in dry periods. Also the current network of nature reserves needs to be reconsidered in the light of climate warming as species are expected to lose climatically suitable areas within the existing protected areas (Araújo *et al.*, 2011). Model projections could support this revision, and the vulnerability index, as proposed in this study, may be a helpful and quantitative tool in prioritizing conservation actions.

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SUPPORTING INFORMATION

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

Appendix S1 Details on the species distribution modelling.

Appendix S2 Definition of the European reservoir.

Appendix S3 Table with the vulnerability indices for all the 166 species of breeding birds assessed for Switzerland.

Appendix S4 Effect of different weightings of the base indicators on the resulting vulnerability index.

BIOSKETCH

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