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Research

Climate-niche factor analysis: a spatial approach to quantifying species vulnerability to climate change

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Climate change vulnerability assessments are an important tool for understanding the threat that climate change poses to species and populations, but do not generally yield insight into the spatial variation in vulnerability throughout a species' habitat. We demonstrate how to adapt the method of ecological-niche factor analysis (ENFA) to objectively quantify aspects of species sensitivity to climate change. We then expand ENFA to quantify aspects of exposure and vulnerability to climate change as well, using future projections of global climate models. This approach provides spatially-explicit insight into geographic patterns of vulnerability, relies only on readily-available spatial data, is suitable for a wide range of species and habitats, and invites comparison between different species. We apply our methods to a case study of two species of montane mammals, the American pika *Ochotona princeps* and the yellow-bellied marmot *Marmota flaviventris*.

Keywords: climate change, ecological-niche factor analysis (ENFA), exposure, *Marmota flaviventris*, *Ochotona princeps*, sensitivity, vulnerability, vulnerability assessment

Introduction

The risk of extinction due to climate change is a significant threat to many species, and is a crisis of global scale (Field et al. 2014). Identifying species vulnerable to climate change and the extent of their vulnerability is vital for guiding effective conservation efforts (Stanton et al. 2015). There are presently more than 1.6 million known species of plants and animals whose global conservation status have not yet been assessed, along with countless millions more 'unknown unknowns' (Mora et al. 2011, Roskov et al. 2014, IUCN 2017), largely due to a lack of relevant biological and ecological data. How are we to assess climate vulnerability when we are faced with a dearth of information? Moreover, how can we assess vulnerability in a timely manner to help facilitate preventative conservation measures that better anticipate risk than traditional diagnostic approaches?

A common framework describes three fundamental aspects of climate change vulnerability: sensitivity, the degree to which the persistence ability of a species is determined by the climatic conditions of its habitat; exposure, the extent to which the species will experience climate change across its range; and adaptive capacity, the ability to adapt to changes in climate, typically through evolutionary responses, dispersal, and phenotypic plasticity (Williams et al. 2008). Several different methods for assessing these three aspects have been proposed, and typically use trait-based species characteristics or climate-modeling approaches to derive coarse indices or categories of vulnerability (Thomas et al. 2011, Young et al. 2012, Foden et al. 2013).

Prior to and seemingly unrelated to these more recent approaches to assessing climate vulnerability, Hirzel et al. (2002) introduced ecological-niche factor analysis (ENFA), a method of quantifying the environmental niche of a species using presence-only data. ENFA has since become a popular tool and has been applied to many types of organisms, including mammals (De Knegt et al. 2011), birds (Loiselle et al. 2010), amphibians (Soares and Brito 2006), and plants (Engler et al. 2004). Although Hirzel et al. (2002) suggested a method for inter-species comparison, few studies have used ENFA to analyze more than one species at a time (but see Reutter et al. 2003, Sattler et al. 2007). It is unclear precisely why, but we are unaware of any studies that draw an explicit conceptual link between ENFA and other methods of vulnerability comparison. As such, we surmise that inter-species comparison is simply an application of ENFA that is as yet poorly explored.

Here we demonstrate how ENFA can be adapted as a tool for assessing climate-change vulnerability, by providing a measure of species sensitivity to climate change. We further show how its methods can be expanded to infer a measure of exposure to climate change from future climate projections. In contrast to other assessment methods, our approach yields spatially-explicit descriptions of climate vulnerability. Moreover, by relying solely on presence-only distribution data and readily-available climate models, our approach avoids the need for detailed life history knowledge and absence data, and can be employed rapidly for a wide variety of species, and in a manner that invites direct comparison of results for different species. We provide a case study that contrasts the climate vulnerability of two species: the American pika *Ochotona princeps*, a small lagomorph with a well-documented sensitivity to climate change, and the yellow-bellied marmot *Marmota flaviventris*, a larger sympatric rodent.

Methods

Hutchinson (1957) described the ecological niche of a species as an n-dimensional hypervolume embedded in the n-dimensional space defined by n ecological variables. ENFA quantifies this niche by comparing the distribution of a species in ecological-space with the larger distribution of available habitat conditions, referred to as the global distribution. The species' niche is primarily described by two quantities: the marginality reflects the location of the species' niche in ecological-space relative to the global distribution, and the specialization reflects the size of the species' niche relative to the size of the global distribution. We direct the reader to Hirzel et al. (2002) and Basille et al. (2008) for more thorough details on the ENFA process, and to Supplementary material Appendix 1 for a more explicit treatment of our approach. Here we will briefly introduce the concepts necessary to develop the remaining portions of this paper.

Marginality

For a set of standardized P environmental rasters with N cells each, let $\mathbf{Z}$ denote the $N \times P$ matrix such that z_{ij} is the standardized value of variable j at location i. The $P \times P$ global covariance matrix is

$$\mathbf{R}_G = \frac{1}{N}\mathbf{Z}^\mathrm{T}\mathbf{Z} \tag{1}$$

We define a unit vector $\mathbf{p}$ of length N that represents habitat utilization by the proportion of presence locations in each cell. The marginalities of P variables may be succinctly written as

$$\mathbf{m} = \mathbf{Z}^\mathrm{T}\mathbf{D_p}\mathbf{1}_N \tag{2}$$

where $\mathbf{1}_N$ is a vector of ones of length N. The vector $\mathbf{m}$ of length P is called the marginality factor. An illustration of a two-dimensional example of $\mathbf{m}$ can be seen in Fig. 1a. We may calculate an overall marginality M from the marginality factor $\mathbf{m}$, which we define as

$$M \equiv \sqrt{\mathbf{m}^\mathrm{T}\mathbf{m}} \tag{3}$$

M can be interpreted as the distance between the centroid of the species' niche and the centroid of the global niche.

Specialization and sensitivity

For a single ecological variable, Hirzel et al. (2002) defined the specialization as

$$s = \frac{\sigma_G}{\sigma_S} \tag{4}$$

where σ_G is the standard deviation of the global distribution, and σ_S is the standard deviation of the species distribution. Generalizing to multiple dimensions, the species covariance matrix $\mathbf{R_S}$ weighted by utilization is given by

$$\mathbf{R_S} = \left(\mathbf{Z} - \mathbf{1}_N\mathbf{m}^\mathrm{T}\right)^\mathrm{T}\mathbf{D_p}\left(\mathbf{Z} - \mathbf{1}_N\mathbf{m}^\mathrm{T}\right) \tag{5}$$
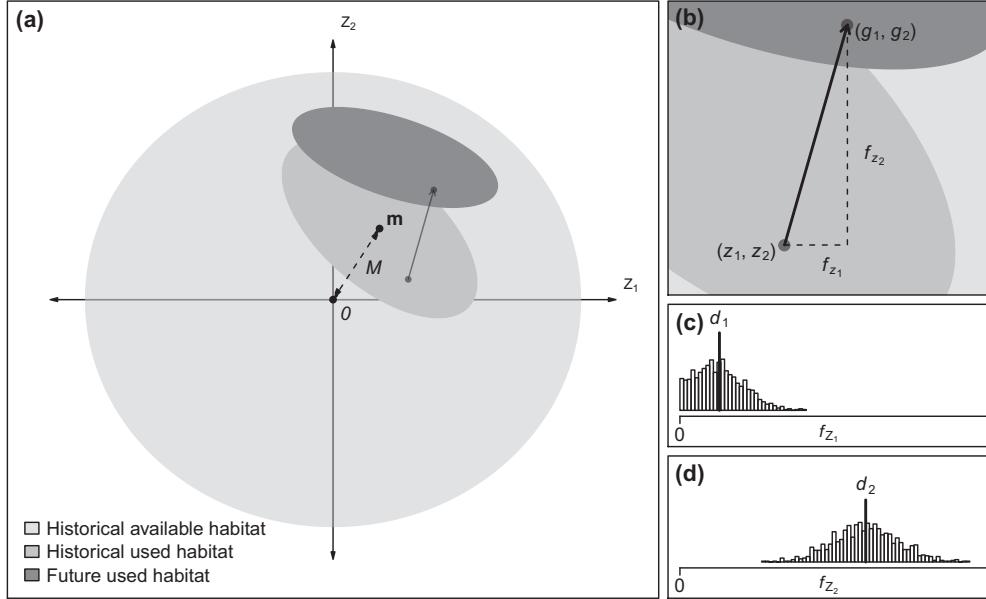
Figure 1. (a) A hypothetical representation of the ecological niche in two uncorrelated climate dimensions. The species occupies a subset of the available habitat, which has been normalized in each dimension. Future changes in climate shift the climate conditions inside the historical species habitat. The distance from the global centroid to the historical habitat centroid is the overall marginality M, with vector $\mathbf{m}$ describing the marginality in each dimension. The solid arrow illustrates the climate shift of a single location. (b) Decomposition of the climate shift of a single location. The absolute differences between the historical coordinates (z_1, z_2) and the future coordinates (g_1, g_2) are given by (f_{Z_1}, f_{Z_2}). (c) and (d) are histograms of the sets of distances f_{Z_1}, f_{Z_2} across all locations. The means of these distances define the departure vector $\mathbf{d} = (d_1, d_2)$.

with $\mathbf{D_p} = \mathrm{Diag}(\mathbf{p})$ as before. ENFA finds the $P-1$ unit vectors $\mathbf{u}$ that maximize the ratio

$$\frac{\mathbf{u}^T\mathbf{R_G}\mathbf{u}}{\mathbf{u}^T\mathbf{R_S}\mathbf{u}} \qquad (6)$$

such that each vector $\mathbf{u}_j$ is orthogonal to $\mathbf{m}$. Each vector $\mathbf{u}_j$ is called a specialization factor, and has an associated eigenvalue λ_j that describes the amount of specialization expressed on that axis.

Different approaches have been suggested for calculating an overall index of specialization S (Hirzel et al. 2002, Bryan and Metaxas 2007), which generally involve a sum of the eigenvalues λ_j. We see two shortcomings of these approaches. First, they neglect to account for the amount of specialization that is expressed on the marginality axis, and thus yield an incomplete measure of specialization (Basille et al. 2008). The marginality axis necessarily reflects some amount of specialization, since a species with higher marginality will have a more constrained habitat. The amount of specialization on the marginality axis is the ratio of the variances of the available habitat to the used habitat projected onto $\mathbf{m}$, given by

$$\lambda_m = \frac{\mathbf{m}^T\mathbf{R_G}\mathbf{m}}{\mathbf{m}^T\mathbf{R_S}\mathbf{m}} \qquad (7)$$

Second, by measuring the amount of specialization in the ENFA factors, this notion of overall specialization is at odds with the notion of overall marginality, which reflects the amount of marginality in each of the environmental variables. We outline a different approach to quantifying the overall specialization that addresses these two issues.

First, we collect λ_m and λ_j together and rename them such that $(\lambda_m, \lambda_1, \ldots, \lambda_{P-1}) = (\rho_1, \rho_1, \ldots, \rho_P)$. Next, let the columns of the $P \times P$ matrix $\mathbf{U}$ be comprised of the niche factors, such that

$$\mathbf{U} = (\mathbf{m}, \mathbf{u}_1, \ldots, \mathbf{u}_{P-1}) \qquad (8)$$

Since $\mathbf{m}$ itself expresses some amount of specialization, each component u_{jk} of $\mathbf{U}$ describes the amount of influence the environmental variable j has on the shape of the species' ecological niche in factor k. The higher the value of u_{jk}, the more restricted the range of the species is in variable j in factor k. We define a left stochastic matrix $\mathbf{V}$ with each column summing to 1, such that

$$v_{jk} = \frac{|u_{jk}|}{\sum_{j=1}^{P}|u_{jk}|} \qquad (9)$$

It follows that, for a given environmental variable j, the quantity

$$s_j = \sum_{k=1}^{P} v_{jk}\rho_k \qquad (10)$$

3

reflects the total specialization found in variable j. If a species is highly constrained in j in the first few factors, for example, s_j will be higher, since the first few factors account for most of the specialization. Conversely, if a population is highly constrained in j in only the last few factors, s_j will be lower, since the last factors account for less specialization. The higher the value of s_j, the more restricted the species' range in variable j. We may calculate the total specialization found in each environmental variable by

$$\mathbf{s} = \mathbf{V}\boldsymbol{\rho} \qquad (11)$$

We call $\mathbf{s}$ the sensitivity factor to distinguish it from other definitions of specialization, and note that

$$\sum_{j=1}^{P} s_j = \lambda_m + \sum_{j=1}^{P-1} \lambda_j \qquad (12)$$

From $\mathbf{s}$, we may also calculate an overall index of sensitivity S as

$$S \equiv \sqrt{\frac{1}{P}\sum_{j=1}^{P} s_j} \qquad (13)$$

Quantifying sensitivity to climate change

In general, the higher the overall climate sensitivity of a species, the smaller the climatic niche that the species inhabits. If a species only tolerates a narrow range of climatic conditions, we may reasonably expect it to be more sensitive to the effects of climate change than a species that is capable of thriving in a wider range of conditions. Thus, when our P environmental variables are all climate variables, the sensitivity factor $\mathbf{s}$ of a species is a direct reflection of its sensitivity in each climate dimension. The overall sensitivity S reflects the average specialization in each variable, and provides a useful measure for comparison between species, provided the same reference study area is used.

The matrix $\mathbf{S}$ comprised of environmental data in locations of species presence can be projected onto the sensitivity axis, with coordinates inside the habitat given by $\boldsymbol{\sigma}_\mathbf{s} = 1/P(|\mathbf{S}-\mathbf{m}|\mathbf{s})$ and coordinates of the study area given by $\boldsymbol{\sigma}_\mathbf{G} = 1/P(|\mathbf{Z}-\mathbf{m}|\mathbf{s})$. A location i of greater climatic extreme relative to mean habitat conditions will have a larger σ_i, and a location closer to the species' climatic means will have a smaller σ_i.

Quantifying exposure to climate change

Climate models are frequently used to predict the extent and magnitude of climate change over the coming century. The differences between present and future conditions inside present-day habitat reflect the amount of climate change a species might experience if it remains in place. Using historical climate data and future climate predictions, we use a dissimilarity measure as a metric of species exposure to climate change.

As before, let z_{ij} represent the scaled historical value of climate variable j at location i. Let g_{ij} be the predicted future value of variable j at location i that is also scale relative to historical values. We denote the absolute difference between $\mathbf{G}$ and $\mathbf{Z}$ as $\mathbf{F}$, with $f_{ij} = |g_{ij} - z_{ij}|$ (Fig. 1b). Weighting by habitat utilization, the average distance between a species' normalized future and historical habitat conditions in variable j is then

$$d_j = \sum_{i=1}^{N} p_i f_{ij} \qquad (14)$$

or, in vector form,

$$\mathbf{d} = \mathbf{F}^\mathrm{T}\mathbf{D}_\mathbf{p}\mathbf{1}_N \qquad (15)$$

We call $\mathbf{d}$ the departure factor (Fig. 1c–d). The higher the value of d_j, the greater the departure from historical conditions in variable j. $\mathbf{F}$ projects onto the departure axis with coordinates $\boldsymbol{\delta} = \mathbf{F}\mathbf{d}$, with larger values of δ_i indicating greater departure in location i. We calculate an overall departure D by

$$D \equiv \sqrt{\mathbf{d}^\mathrm{T}\mathbf{d}} \qquad (16)$$

D is a measure of the change between historical and future climate values within the species' historical habitat. We note that D is not simply the distance between the historical and future centroids of the species due to the absolute value; this definition ensures that $D > 0$ whenever there is a change between future and historical values, regardless of whether the average difference is 0. D and $\boldsymbol{\delta}$ are consistent with the concept of exposure in our climate change vulnerability framework, and as such, do not necessarily reflect the extent to which the changes in climate will affect the population.

Quantifying vulnerability to climate change

Putting aside the potential influence of adaptive capacity, vulnerability to climate change reflects the interaction between sensitivity and exposure to climate change. The geometric mean

$$v_j = \sqrt{(1 + d_j)s_j} \qquad (17)$$

then, can be interpreted as a measure of the vulnerability of the population in variable j. Larger values of s_j and d_j indicate higher climate specialization and departure, respectively, which result in a larger v_j, indicating higher vulnerability in variable j. Conversely, smaller values of either s_j or d_j will result in a smaller v_j. No departure and no sensitivity results

in $v_j = 1$. The vulnerability for each climate variable is given by the vulnerability factor **v**, written as

$$\mathbf{v} = \left(\mathbf{D_{d+1}} \mathbf{V} \boldsymbol{\rho} \right)^{\frac{1}{2}} \quad (18)$$

where $\mathbf{D_{d+1}} = \mathrm{Diag}(\mathbf{d}+\mathbf{1})$. The vulnerability axis with coordinates $\boldsymbol{\nu}$ is calculated by

$$\nu_i = \sqrt{\delta_i \sigma_i} \quad (19)$$

We define the overall vulnerability as

$$V \equiv \sqrt{\frac{1}{P} \sum_{j=1}^{P} v_j} \quad (20)$$

Equation 17 gives equal weight to the influence of sensitivity and exposure, but this need not be the case. More generally, we may use the weighted geometric mean

$$v_j = \left((1+d_j)^m s_j{}^n \right)^{\frac{1}{m+n}} \quad (21)$$

with m and n reflecting the relative weights of exposure and sensitivity, respectively. The coordinates on the vulnerability axis $\boldsymbol{\nu}$ then become

$$\nu_i = \left(\delta_i{}^m \sigma_i{}^n \right)^{\frac{1}{m+n}} \quad (22)$$

Implementation in R

Rinnan (2018) authored the 'CENFA' R package to provide tools to implement the methods that we have outlined here. The 'CENFA' package is available on the CRAN repository at <https://CRAN.R-project.org/package=CENFA>. It is designed to work with spatial data directly – including raster, shapefile, and point data formats – and to handle large datasets efficiently via partial data loading and parallelization.

Case study: applications to the American pika and the yellow-bellied marmot

The American pika *Ochotona princeps* is a small lagomorph that inhabits talus and scree slopes throughout mountain ranges in western North America, and some lower-elevation habitat in rocky sections of waterways such as the Columbia River Gorge. Pikas are quite sensitive to high temperatures, and are widely recognized as being threatened by climate change due to loss of habitat associated with warming

(Moritz et al. 2008, Erb et al. 2011). Despite evidence of range contraction and population declines (Beever et al. 2003), the IUCN's Red List of threatened species database presently categorizes the American pika as a species of Least Concern (IUCN 2017).

The yellow-bellied marmot *Marmota flaviventris* shares considerable habitat overlap with the American pika, but any sensitivity to climate change is less evident. One simple explanation for this is that marmots hibernate and pikas do not, and perhaps marmots are therefore less impacted by climate change that takes place during hibernation. Although climate-related phenological shifts in hibernation emergence and body size have been documented (Inouye et al. 2000, Armitage 2013), there is concomitant evidence of increases in survival rates, body size, and population (Ozgul et al. 2010). The IUCN's Red List also categorizes this species of marmot as one of Least Concern, with no major recognized threats (IUCN 2017).

For our analysis, we used climate datasets consisting of bioclimate variables (Table 1) at a 30 arc-second resolution (~1 km) from the WorldClim database (Hijmans et al. 2005). We chose 10 of the 19 bioclimate variables to represent a broad range of seasonal and annual climatic patterns across the study area while minimizing redundancy. The historical dataset was based on climate records averaged from 1960 to 1990. Future projections for 2050 (averages from 2041 to 2060) were derived from the MIROC5 global climate model for two different representative concentration pathways (RCP4.5 and RCP8.5) (Stocker 2014). Digital maps of pika and marmot habitat were obtained from the IUCN's Red List of threatened species database (IUCN 2017) and rasterized to the same resolution as the climate data. We interpreted these habitat rasters as presence data with equal utilization weights for all cells in which the species were present. The global study area was cropped to the union of the extent of the two species' ranges. All data processing and analysis was done in R ver. 3.5.1 (<www.r-project.org>).

Relative to the study area, pika habitat is much cooler during the warm seasons, receives considerably more precipitation during the dry season, and experiences less temperature fluctuation (see the marginality factor in Table 2a). Pikas are most sensitive to variables associated with seasonal temperature extremes, daily temperature fluctuations, and the amount of precipitation in the wettest periods (sensitivity factor in Table 2a). An overall marginality M of 1.840 shows that pika habitat is substantially different from the mean climate conditions in the study area, and an overall sensitivity S of 2.111 shows that the range of pika's tolerable climate conditions are quite restricted, with the greatest sensitivity to hot and cold temperature extremes. Although pikas appear relatively sensitive to changes in mean diurnal temperature range (MDR), the MDR departure was quite small, leading to moderate MDR vulnerability. Conversely, although there was substantial departure in precipitation seasonality (PS), pikas showed a low sensitivity to PS, and so overall PS vulnerability was relatively low.

Table 1. Bioclimatic variables used for this study, obtained from the WorldClim database (Hijmans et al. 2005), and derived from monthly measurements of temperature and precipitation.

HM_{max}	max temp of warmest month (°C)
CM_{min}	min temp of coldest month (°C)
PS	precip seasonality (SD/mean monthly precip)
TS	temp seasonality (SD monthly temp × 100)
PWM	precip of wettest month (mm)
PDM	precip of driest month (mm)
PWQ	precip of wettest quarter (mm)
PDQ	precip of driest quarter (mm)
MDR	mean diurnal range (mean of monthly max temp − min temp)
ISO	isothermality ($MDR/(HM_{max} - CM_{min}) \times 100$)

Pikas appear most vulnerable to thermal extremes in the hottest and coldest months (HM_{max} and CM_{min}), reflecting their well-documented sensitivity to extreme temperatures (Moritz et al. 2008, Beever et al. 2011).

With an overall marginality M of 1.026, by contrast, marmot habitat is not appreciably different from the global means of the study area, but is generally characterized by greater differences in the mean diurnal range, warmer extremes, and less precipitation during the wet season (Table 2b). An overall sensitivity S of 2.554, however, suggests a narrower climate-niche than pika, with the greatest restrictions in wet-season precipitation (PWM and PWQ) and cold-season temperature extremes (CM_{min}). These sensitivities agree with other characterizations of the yellow-bellied marmot's climatic niche (Schwartz and Armitage 2005, Armitage 2013).

The RCP8.5 scenario had greater departure than the RCP4.5 scenario in almost every variable, reflecting the expected increase in climate change associated with the concentration of greenhouse gas emissions (Stocker 2014). Overall pika departures D were 0.808 (RCP4.5) and 0.944 (RCP8.5). This led to a higher overall vulnerability in the RCP8.5 scenario ($V = 1.265$) than the RCP4.5 scenario ($V = 1.259$). Vulnerability was calculated with Eq. 17, giving equal weights to sensitivity and exposure.

Marmots demonstrated even more vulnerability to thermal extremes than pikas, as a result of relatively high sensitivity and departure to HM_{max} and CM_{min}. Overall marmot departures D were comparatively lower, with $D = 0.774$ (RCP4.5) and 0.895 (RCP8.5). Despite this, marmots had slightly higher overall vulnerability than pikas in both scenarios, with $V = 1.316$ (RCP4.5) and 1.310 (RCP8.5).

We used the projected coordinates σ, δ, and ν to visualize spatial variation in sensitivity, exposure, and vulnerability for the RCP4.5 scenario, both within species habitat (Fig. 2) and for the entire study area (Fig. 3). The most vulnerable current pika habitat appears in the Cascades, the northern Rockies, and the Great Basin region, corresponding with observations of high rates of extirpation and habitat loss (Beever et al. 2011). The most vulnerable current marmot habitat is located throughout the Cascades, the Great Basin, and an isolated population in the Badlands of South Dakota. Predictions suggest that regions adjacent to the Canadian

Table 2. The first three CNFA factors for (a) *O. princeps* and (b) *M. flaviventris*, and the resulting sensitivity factors **s**, departure factors **d**, and vulnerability factors **v**, calculated for 2050 MIROC5 GCM projections under two different RCPs (4.5 and 8.5). Bioclimate variables are listed in decreasing magnitude of the coefficients of **v**. Bold values indicate the five coefficients with the largest magnitude in each column. The amount of specialization in each CNFA factor is in parentheses.

Bioclimate variable	Marg.	Spec. 1	Spec. 2	Sens.	Dep. (RCP4.5)	Dep. (RCP8.5)	Vuln. (RCP4.5)	Vuln. (RCP8.5)
(a) *Ochotona princeps*	(7.5%)	(36.1%)	(18.6%)					
CM_{min}	**0.05**	0.66	0.36	**2.74**	0.34	0.43	**1.92**	**1.98**
HM_{max}	**−0.72**	**0.41**	−0.31	**2.39**	**0.48**	**0.61**	**1.88**	**1.96**
PWM	0.22	−0.04	**−0.38**	**2.23**	**0.23**	**0.22**	**1.65**	**1.66**
PWQ	0.23	0.10	**0.38**	**2.24**	0.19	0.20	**1.63**	**1.64**
ISO	0.25	**0.37**	**−0.52**	**2.31**	0.11	0.11	**1.60**	**1.60**
MDR	−0.19	**−0.44**	**0.46**	**2.33**	0.07	0.08	1.58	1.59
PDQ	**0.93**	−0.08	0.08	1.68	0.19	0.21	1.42	1.43
PDM	**0.93**	0.04	−0.07	1.55	**0.27**	**0.29**	1.40	1.41
TS	**−0.63**	**−0.21**	0.01	1.84	0.06	0.07	1.40	1.41
PS	**−0.74**	−0.06	0.05	1.39	**0.29**	**0.31**	1.34	1.35
(b) *Marmota flaviventris*	(9.3%)	(27.3%)	(19.6%)					
CM_{min}	0.20	**−0.30**	**0.57**	**3.03**	**0.39**	**0.47**	**2.05**	**2.11**
HM_{max}	**0.28**	0.28	**−0.39**	**2.76**	**0.51**	**0.62**	**2.05**	**2.12**
PWM	**−0.35**	**0.51**	−0.22	**3.18**	0.13	0.12	**1.89**	**1.89**
PWQ	−0.34	**−0.44**	0.26	**3.08**	0.09	0.10	**1.83**	**1.84**
ISO	**0.38**	**0.38**	**−0.44**	2.66	**0.14**	**0.15**	**1.74**	1.75
MDR	**0.52**	**−0.30**	**0.43**	**2.71**	0.12	0.13	**1.74**	**1.75**
PDQ	−0.08	−0.26	−0.08	2.16	0.10	0.11	1.54	1.55
PDM	−0.08	0.27	0.11	2.00	**0.17**	**0.17**	1.53	1.53
TS	−0.25	−0.06	0.12	1.96	0.07	0.07	1.45	1.45
PS	**−0.46**	−0.01	0.03	1.37	**0.29**	**0.29**	1.33	1.33

Rockies may provide suitable refuge from climate change for pika, but less so for marmots. In contrast, climate refuge in eastern Colorado and isolated patches of the southwest will likely be more amenable to marmots than pikas.

Discussion

Climate–niche factor analysis (CNFA) quantifies different aspects of the climatic niche of a species. There are several other such factor analysis methods that have been used to describe environmental niches, including the MADIFA, a factorial decomposition based on the Mahalanobis distance (Calenge et al. 2008), and the GNESFA, which provides a generalized framework of niche factor analysis (Calenge and Basille 2008). The differences between these approaches arise primarily from how the species data are transformed relative to the reference habitat. CNFA could likely be adapted to these other factor analyses as well, but we have not yet explored this possibility. For the purposes of inter-species comparisons, however, we recommend using a framework that centers the data on the shared reference habitat to better facilitate direct comparison, such as CNFA or FANTER, a similar factor analysis method for multimodal niches (Calenge and Basille 2008).

There are several important distinctions between CNFA and ENFA. First, traditional implementations of ENFA may incorrectly calculate the amount of specialization on the marginality axis due to an error in the formulation of the species covariance matrix (Supplementary material Appendix 1). Fortunately, this is easily fixable. Second, the sensitivity factor $\mathbf{s}$ as we've defined it provides a fundamentally different characterization of specialization than the ENFA's specialization factor. The sensitivity factor expresses the amount of specialization in each climate dimension, rather than the amount in each factor, making it more directly analogous to the marginality factor. It also does not neglect to account for the amount of specialization on the marginality axis. We maintain that this provides a more meaningful, intuitive, and useful measure of climate sensitivity. Finally,
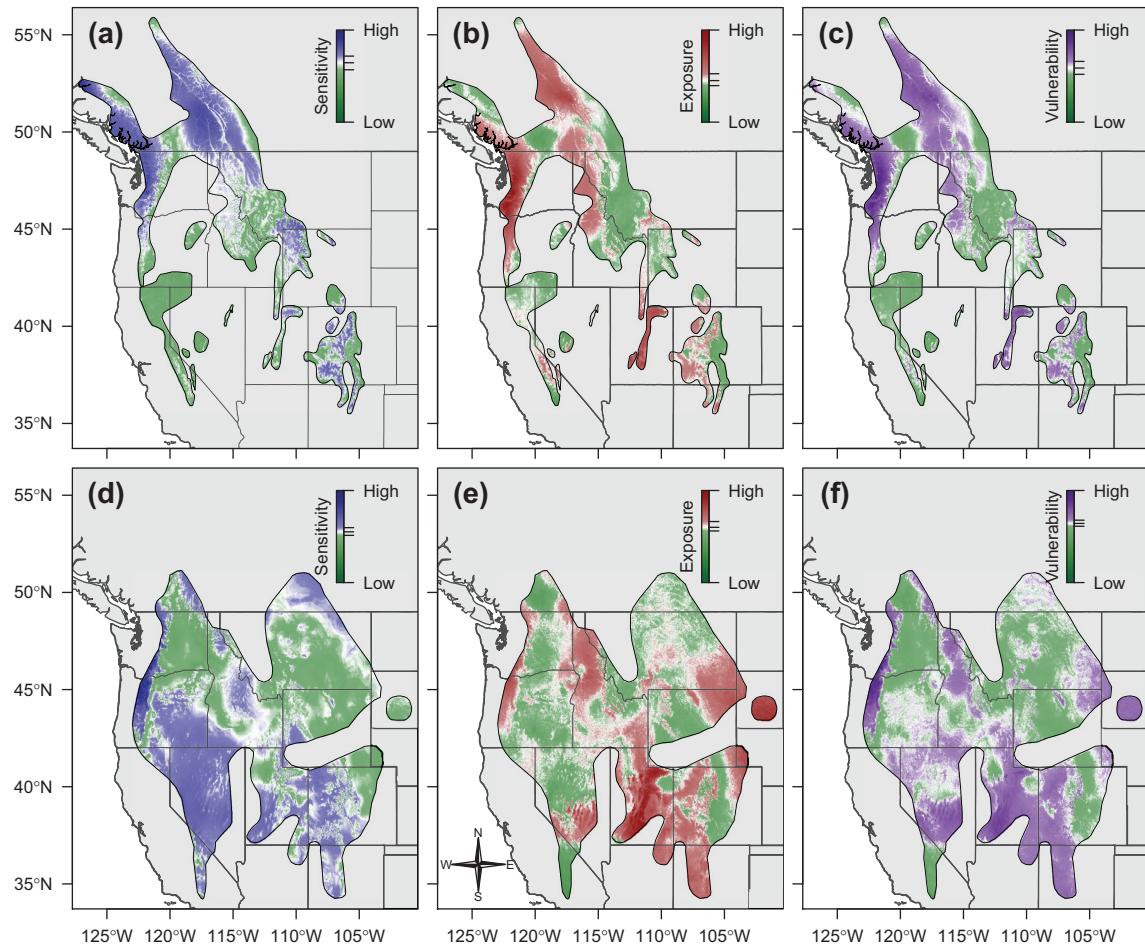

Figure 2. (a) Sensitivity, (b) exposure and (c) vulnerability across the habitat of *O. princeps*, and (d) sensitivity, (e) exposure, and (f) vulnerability across the habitat of *M. flaviventris* for the MIROC5 RCP4.5 climate scenario. Sensitivity values are given by $\boldsymbol{\sigma_s} = 1/P(|\mathbf{S} - \mathbf{m}|\mathbf{s})$; exposure values by $\boldsymbol{\delta_s} = \mathbf{F_s}\mathbf{d}$, with $\mathbf{F_s}$ representing the values of $\mathbf{F}$ inside the habitat; and vulnerability by $\mathbf{v_s} = \sqrt{\mathbf{D_{\delta_s}}\boldsymbol{\sigma_s}}$, with $\mathbf{D_{\delta_s}} = \text{Diag}(\boldsymbol{\delta_s})$. Tick marks on the legend axes represent quantile breaks.
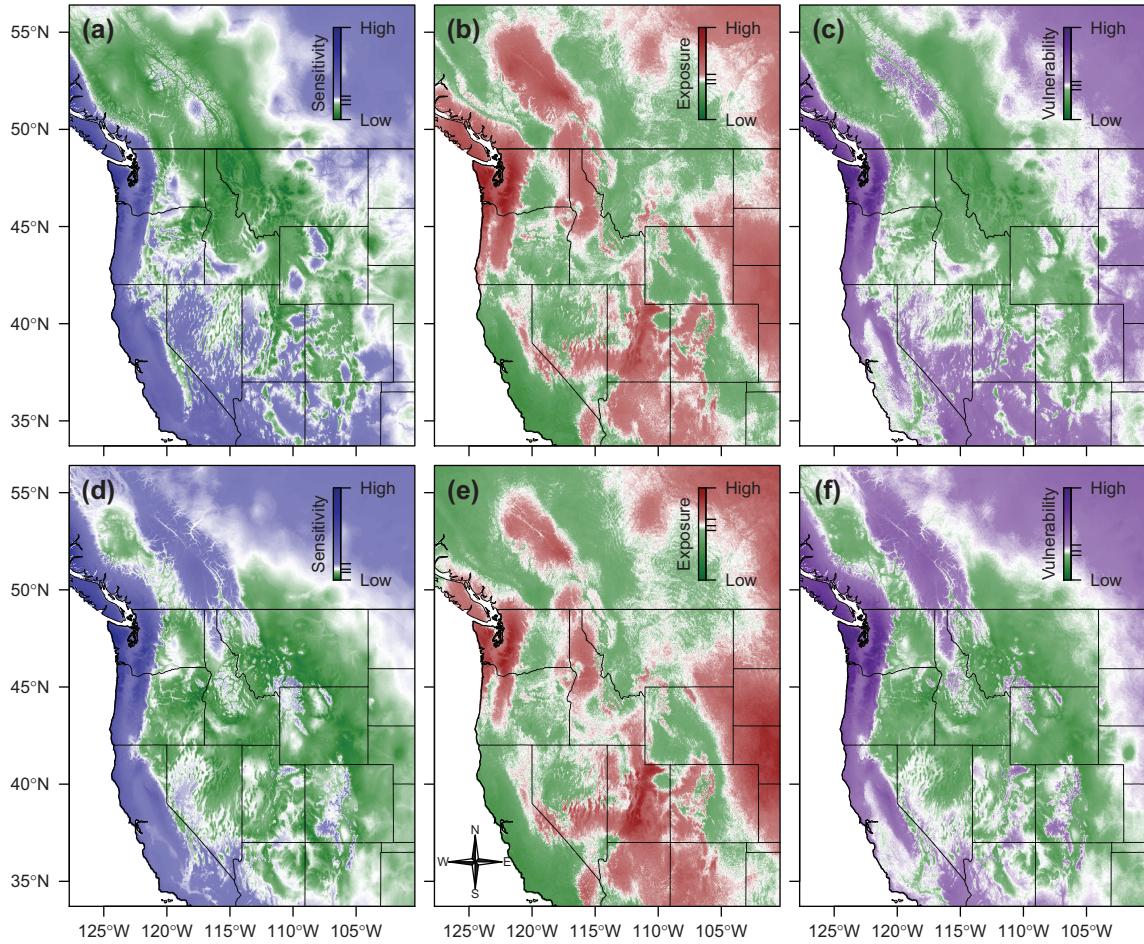
Figure 3. (a) Predicted sensitivity, (b) exposure and (c) vulnerability of *O. princeps*, and (d) sensitivity, (e) exposure and (f) vulnerability across of *M. flaviventris* across the entire study area for the MIROC5 RCP4.5 climate scenario. Sensitivity values are given by $\sigma_G = 1/P|Z - m|s$; exposure values by $\delta_G = Fd$; and vulnerability by $v_G = \sqrt{D_{\delta_G}\sigma_G}$, with $D_{\delta_G} = \text{Diag}(\delta_G)$. Tick marks on the legend axes represent quantile breaks.

CNFA provides a novel method for quantifying exposure to climate change by applying the factor analysis to future climate scenarios.

The IUCN Red List's criteria for conservation assessment have been criticized for not adequately accounting for climate-related threats to species (Thomas et al. 2004, Thuiller et al. 2005). A formal assessment of extinction risk is often a necessary step to give a species the recognition it needs to kickstart conservation actions, but this can be a slow process. By the time criteria such as population decline or range contraction are directly observable at a population level, it may already be too late for meaningful and effective conservation actions (Hannah 2011). At a minimum, vulnerable species must be identified as early as possible to maximize the chances for successful conservation (Stanton et al. 2015). One of the strengths of our approach is the ability to identify and describe aspects of climate sensitivity and exposure to climate change with relatively little information about the species itself. This enables us to more proactively identify species of highest climate vulnerability and species in need of

immediate conservation actions. Moreover, CNFA provides a formal method for inter-species comparison, which could be used to prioritize species assessments.

The American pika is an example of a species with a well-documented sensitivity to climate change. Our case study found that yellow-bellied marmots have a narrower climate-niche than pikas, which suggests that they may in fact be more sensitive to climate change than pikas. One possible explanation for this is that marmots only find a narrow range of climatic conditions suitable for hibernation, supported by the observation that the three largest components of the marmot's sensitivity factor are all associated with winter climate variables (CM_{min}, PWM, PWQ). Marmots will experience slightly less overall exposure to climate change within their habitat, though, and there is some evidence that this change may benefit the species (Ozgul et al. 2010). The climate vulnerability framework that we used to motivate our approach contained three fundamental axes. Depending on each species' capacity to adapt to climate change via dispersal, rapid evolution or other processes, we would place them on

a spectrum between 'at-risk adapters' (i.e. highest adaptive capacity) and 'highly vulnerable' (i.e. low adaptive capacity) (Foden et al. 2013). Recommended actions involve monitoring the populations and supporting adaptive responses, prioritizing the geographic locations in which vulnerability is greatest. By identifying the climate dimensions of sensitivity and exposure, these actions can be directed toward the geographic locations of greatest vulnerability, which may better detect early signs of climate-related population impacts.

It is important to note, however, that by neglecting to include other ecological processes that shape habitat, our approach suffers from some of the shortcomings common to species distribution models (Lawler et al. 2006). One such issue is that our conclusions are based on an analysis of the realized niche of a species rather than its fundamental niche. Non-climatic constraints such as biotic interactions, dispersal ability, and landscape topography can prevent a species from populating habitat that is climatically suitable (Jiménez-Valverde et al. 2008). Future novel climates might also favor a species, despite differing from the climate the species currently experiences (Fitzpatrick and Hargrove 2009). Another issue is that CNFA quantifies the magnitude of sensitivity and exposure, but not the direction. A habitat location i with high σ_i indicates a place of climatic extreme, but the vulnerability ν_i of i does not reflect whether the expected climate departure δ_i will shift toward or further away from the means. The direction of change can be derived from the raw climate values $\mathbf{Z}$ and $\mathbf{G}$, but this is an area that needs further development.

Species with disjoint populations or localized adaptations to their environment may have multimodal environmental niches. An analysis that neglects differences in niche constraints of distinct subpopulations may underestimate the climate vulnerability of the species. In these cases, it may be more appropriate to perform an analysis at the subspecies or subpopulation level. One such example is the spotted owl *Strix occidentalis*, with three geographically distinct subspecies. At the species level CNFA would likely describe a much broader spotted owl climatic niche that stretches from southwestern British Columbia to the Sierra Madres in Mexico, ignoring the climatic adaptations of each subspecies. Similarly, overestimates of vulnerability may occur for highly mobile or migratory species that follow seasonal changes in climate.

CNFA only provides relative comparisons between species, not absolute. Determining thresholds of sensitivity or departure to categorize a species as low or high risk is highly contextual, and may differ greatly between taxa. As general rules of thumb, we suggest that inter-species comparisons are better suited to species that are more closely related to one another, and that vulnerability thresholds be assessed by species class or any more specific taxonomic rank.

Climate change affects species in myriad ways, and the same environmental stimuli can induce completely different responses in different species. Non-climatic processes may impose constraints that correlate with climate variables, further obscuring accurate niche characterization. Fortunately, there is nothing about CNFA that intrinsically depends on climate, per se. It is readily possible to include non-climatic variables (e.g. soil type, human encroachment) as part of the analysis, provided one has future projections commensurate with the climate scenarios that are used to calculate vulnerability.

Finally, it is possible that CNFA simply provides an inadequate or incorrect characterization of climate vulnerability for some species due to issues of scale and uncertainty. There is often a large disparity between the range maps that delineate species habitat and the distribution patterns of individuals contained therein (Hurlbert and Jetz 2007). The results of CNFA will necessarily preserve the uncertainty associated with the distribution data that was used for the analysis. Our examples for the American pika and the yellow-bellied marmot used range maps as a first step, but could be further refined by using point presence or abundance data, which provide more accurate descriptions of distribution patterns and habitat utilization. The foundation of CNFA would benefit a great deal from further experiments of model validation, including applications to species in which climatic relationships with habitat are already known (Kearney and Porter 2009), and simulation studies in which the relationships are specified a priori. Likewise, the results will necessarily vary with the resolution and extent of analysis. More investigation is needed to examine the scale-dependence of CNFA.

A measure of caution, therefore, is appropriate when using CNFA to inform prescriptive actions. By no means do our methods claim to provide a comprehensive assessment of climate vulnerability. Adaptive capacity is an integral component of overall vulnerability that CNFA does not attempt to address. Although much information can be inferred from spatial vulnerability maps, these inferences are only meaningful as they relate to an organism's ecology and natural history, for which there is no substitute.

When used in tandem with other assessment methods such as climatic niche models (Thomas et al. 2004) or trait-based assessments (Foden et al. 2013), our approach can help provide a more complete, spatially-explicit picture of species vulnerability. CNFA can be used to highlight geographic regions of species vulnerability, inform resource management decisions, and direct conservation efforts. Incorporating our methods into IUCN conservation assessments and other vulnerability assessments may enhance our understanding of species climate risks and facilitate the assessment of unevaluated species.

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Supplementary material (available online as Appendix ecog-03937 at <www.ecography.org/appendix/ecog-03937>). Appendix 1