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RESEARCH ARTICLE

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Global change on the roof of the world: Vulnerability of Himalayan otter species to land use and climate alterations

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Abstract

Aim: Climate Change Vulnerability Assessment (CCVA) prescribes the quantification of species vulnerability based on three components: sensitivity, adaptive capacity and exposure. Such assessments should be performed through combined approaches that integrate trait-based elements (e.g., measures of species sensitivity such as niche width) with correlative tools quantifying exposure (magnitude of changes in climate within species habitat). Furthermore, as land use alterations may increase climate impacts on biodiversity, CCVAs should focus on both climate and land use change effects. Unfortunately, most of such assessments have so far focused exclusively on exposure to climate change.

Location: Himalaya.

Methods: We evaluated the vulnerability of three otter species occurring in the Himalayan region, that is, *Aonyx cinereus*, *Lutra lutra* and *Lutrogale perspicillata*, to 2050 climate and land use change through the recently proposed Climate Niche Factor Analysis (CNFA) framework combined with Species Distribution Models.

Results: Future climate and land use change will reduce (6%–15%) and shift (10%–18%) the geographical range of the three species in the Himalaya, with land use alterations exerting far more severe effects than climate change. Among vulnerability components, sensitivity played a greater role than exposure in determining the vulnerability of the otters. Specifically, the most specialist species, *L. perspicillata*, showed the highest vulnerability in comparison with the most generalist, *L. lutra*.

Main conclusions: Our results underline how coupling climate and land use change components in CCVAs can generate diverging predictions of species vulnerability compared to approaches relying on climate change only. Moreover, intrinsic components, such as species sensitivity, proved significantly more important in determining vulnerability than extrinsic metrics such as habitat exposure.

Pushpinder S. Jamwal and Mirko Di Febbraro should be considered joint first author.

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KEYWORDS
climate change, climate change vulnerability assessment, climate niche factor analysis, habitat exposure, land use change, niche width, SDMs, species distribution models

1 | INTRODUCTION

Climate change has recently emerged as a key threat to biodiversity and ecosystems (Chen et al., 2011; Pacifici et al., 2015). In fact, it is expected to surpass habitat loss as the prime threat to global biodiversity in the future (Leadley, 2010). Besides climate alterations, land use change is among the most critical drivers of global change and biodiversity loss (Lambin, 1999) as it influences many aspects of geo-environmental systems (Guzha et al., 2018; Kiruki et al., 2017; Rogora et al., 2018), hampering the capacity of species to move to suitable habitats (Oliver et al., 2015; Pereira et al., 2012). Despite that, the majority of studies exploring species' responses to global change have largely disregarded the role of land use characteristics, assuming that species are limited only by the shift of climatic conditions (Pacifici et al., 2015; Sirami et al., 2017; but see Di Febbraro et al., 2019). Overall, our current knowledge of the implications of climate and land use change interactions on ecological systems is limited and mainly founded on broad assumptions rather than on observed interactions (Brook et al., 2008; Oliver & Morecroft, 2014). As land use change is expected to increase climate change impacts on biodiversity, it is critical to integrate these two components to understand likely consequences of such pressures on biodiversity (Sirami et al., 2017; Titeux et al., 2017).

From this perspective, an effective assessment of global change threats to biodiversity relies on identifying highly vulnerable species, together with the drivers of such vulnerability. One of the most comprehensive frameworks developed to assess species vulnerability to climate change is the "Climate Change Vulnerability Assessment" (CCVA; Foden et al., 2019). This analytical framework uses an array of different approaches (i.e., biological traits, correlative and mechanistic models) to quantify species vulnerability based on three main components: (a) sensitivity (i.e., degree to which a species is affected by climate change as a consequence of intrinsic attributes such as niche specialization, environmental tolerance, etc.); (b) adaptive capacity (i.e., ability to adjust to climate change by virtue of high levels of phenotypic plasticity, dispersal ability or genetic diversity) and; (c) exposure (i.e., rate and magnitude of climate changes within species habitat; Foden et al., 2019). Despite CCVAs having been widely used in recent years, most of these assessments have focused solely on the exposure component (Thompson et al., 2015), usually quantified through correlative approaches (i.e., Species Distribution Models, "SDMs" hereafter; Pacifici et al., 2015). On the other hand, assessments involving a strictly trait-based approach (i.e., using species' biological characteristics, such as niche width or dispersal capabilities, as predictors of climate-driven extinction risk), mostly quantified species vulnerability according to direct observations, published literature or expert judgment (Borges et al., 2019), though precise vulnerability thresholds associated with each trait are often unknown (Pacifici et al., 2015). Several authors underlined the advantages of using combined approaches able to assess vulnerability by integrating for example, correlative and trait-based elements (Foden et al., 2019; Pacifici et al., 2015). Yet, such compound frameworks have thus far only been used in a limited number of studies (but see e.g., Garcia et al., 2014; Warren et al., 2018), especially if compared to those based solely on correlative models (Pacifici et al., 2015). Along with this general recommendation towards the use of combined approaches, a deeper understanding of how climate change and other pressures, such as land use alterations, could interact to affect the future survival of species was highlighted as another major challenge, as well as a better integration of this interplay in CCVA techniques (Foden et al., 2019).

Vulnerability assessments are particularly crucial in mountain environments, which are amongst the most sensitive ecosystems to global change (Beniston, 2003). Temperatures in the Himalaya, for instance, are increasing at twice the average warming rate of the northern hemisphere (Chen et al., 2009). Increasing climate change impacts, followed by rising resource demands of growing populations, cause serious concerns about the future of Himalayan biodiversity (Chakraborty et al., 2018). Under the current combination of accelerating global warming and habitat degradation and loss, many Himalayan species may not be able to adapt to such overwhelming pressures (Xu et al., 2009).

In mountain ecosystems, global climate change can exert its strongest effects on freshwater habitats (e.g., increased extreme flooding and erosion; Cianfrani et al., 2018). These systems are already heavily affected by anthropogenic factors, such as pollution, dam construction and habitat disturbance. Otters are highly vulnerable species, sensitive to habitat loss and water pollution (Kruuk, 2006; Ruiz-Olmo et al., 1998). As keystone aquatic predators, otters are considered as indicator species of healthy freshwater ecosystems (Kruuk, 2006; Ruiz-Olmo et al., 1998). The Himalaya encompasses the altitudinal range edge of three otter species (Figure S1): the Small-clawed otter (*Aonyx cinereus*), the Eurasian otter (*Lutra lutra*) and the Smooth-coated otter (*Lutrogale perspicillata*; Duplaix & Savage, 2018). The IUCN Red List classifies *L. lutra* as Near Threatened (NT), and *A. cinereus* and *L. perspicillata* as Vulnerable (VU; Duplaix & Savage, 2018; see also Appendix S1). Effects of climate change on the three species have been modelled at large scale by Cianfrani et al. (2018), combining species sensitivity, habitat exposure and other metrics to calculate a global vulnerability index. Also, land use and anthropogenic disturbance were considered as static factors by Cianfrani et al. (2011) to evaluate the effects of climate change on the future distribution of the Eurasian otter in Europe. Investigating how these species could respond to future climate and land use change in a highly vulnerable area such as the Himalaya represents a crucial task for delineating effective conservation strategies against global change impacts. In

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addition, this particular context represents a unique opportunity to test innovative, combined approaches to assess species vulnerability to multiple global change drivers (i.e., climate and land use), in keeping with the prevailing future perspectives delineated for CCVAs (Foden et al., 2019).

In this scenario, the present study aims to explore determinants of otter species vulnerability to future climate and land use change in the Himalaya in terms of species sensitivity (i.e., a measure of niche specialization) and habitat exposure (i.e., dissimilarity between current and future environmental conditions within species habitat). Specifically, we formulated two hypotheses: (i) including land use change in vulnerability assessments yields higher vulnerability values than assessments relying only on climate change; (ii) species sensitivity exerts a significantly higher contribution than habitat exposure in determining vulnerability values. To test these hypotheses, we have adopted the recently proposed "CNFA" (Climate Niche Factor Analysis) framework (Rinnan & Lawler, 2019) combined with state-of-the-art SDMs. In particular, we explicitly integrated SDMs into the "CNFA" framework by calculating species sensitivity and habitat exposure within the presence/absence maps predicted by SDMs.

Specific objectives of this study were: (a) to model the current potential distribution of the three otter species in the Himalaya, considering different combinations of topographic, climatic and land use variables, (b) to predict their potential distribution in 2050 under climate and land use change scenarios, (c) to assess the percentage of gain/loss in range area and the degree of shift experienced by the three species under such scenarios, (d) to assess species vulnerability to these global change scenarios by coupling SDMs and the "CNFA" framework and (e) to quantify the relative contribution of species sensitivity and habitat exposure in shaping vulnerability.

2 | METHODS

2.1 | Analytical framework

To evaluate the effect of climate and land use change on the three species of interest, we modelled their distribution considering present-day environmental conditions under two alternative setups: (i) including only topographic and climate predictors (climate SDMs), and (ii) adding also land use variables (full SDMs). Subsequently, we projected climate SDMs under two 2050 climate change scenarios (IPCC, 2013), and full SDMs by including two additional 2050 land use change scenarios (Li et al., 2017). Predictions from both climate and full SDMs were then used alternatively to quantify range net change and shift, as well as included into the "CNFA" framework to calculate species sensitivity, habitat exposure and vulnerability.

2.2 | Study area

We set our study in the Himalayan region encompassing the following Asian countries: Bhutan, Nepal and some parts of India and Myanmar. The Himalaya is a vast mountain region located between the Indian Subcontinent in the south and the Tibetan Highland in the north. The region extends from Afghanistan in the northwest (36°N and 70°E) to China in the southeast (26°N and 100°E), covering an area of more than 1,000,000 km^2 with a length of 3,000 km and a maximum width of 400 km. The climate ranges from a tropical zone in the lowlands of India and Nepal, to permanent ice and snow at the highest elevations, and from a more continental regime in the northwest to a more oceanic regime in the southeast. Its abruptly rising mountains result in a high diversity of ecosystems and species, characterizing this area as a unique biodiversity hotspot (Xu et al., 2019).

2.3 | Species occurrence data

Occurrence records were gathered from the literature and from online databases, as well as published technical reports (full data source list is provided in Appendix S2). We cross-checked all the occurrences excluding those with a minimum geographical precision coarser than 1 km and collected before 1970, as well as those referring to captive specimens (Cianfrani et al., 2018). Moreover, we drop any occurrence falling farther than 1 km from the hydrographical network (as provided by Lehner et al., 2008). Although opportunistic records may yield accurate predictions of species distribution (Tiago et al., 2017), they are often spatially autocorrelated and/or discontinuous due to a usually unknown and unbalanced sampling effort that can vary noticeably across space (van Strien et al., 2013). Hence, the occurrence dataset for SDMs calibration, which originally included 229 records among the three species, underwent a further filtering procedure to remove clustered data (Appendix S3). After this step, we obtained a final dataset of 12 records for *A. cinereus*, 59 records for *L. lutra* and 43 records for *L. perspicillata* (Figure 1).

2.4 | Environmental predictors

As environmental variables, we considered the 19 Worldclim predictors, along with two topographical and seven land use variables, all rasterized at a resolution of about 1 km. We derived land use variables from the GeoSOS global database (Li et al., 2017; http://geosimulation.cn/GlobalLUCCProduct.html), which describes remotely sensed land use categories as detected by MODIS in 2010 (product MCD12Q1; https://lpdaac.usgs.gov/). In particular, for each pixel we calculated the Euclidean distance from each of these land-use categories. In addition, we calculated the alpha diversity (i.e., count) of land use categories by applying a moving window approach. Specifically, the count of each category was calculated within a 10-km radius circular window moved throughout each pixel of the land use map. Such radius length was coherent with the average home range size of the three species (Kruuk, 2006). Topographical variables included elevation (gathered from Jarvis et al., 2008) and slope (derived from the elevation map). Predictors were further subselected by checking for multicollinearity (VIF ≤5), retaining the following 13 covariates:

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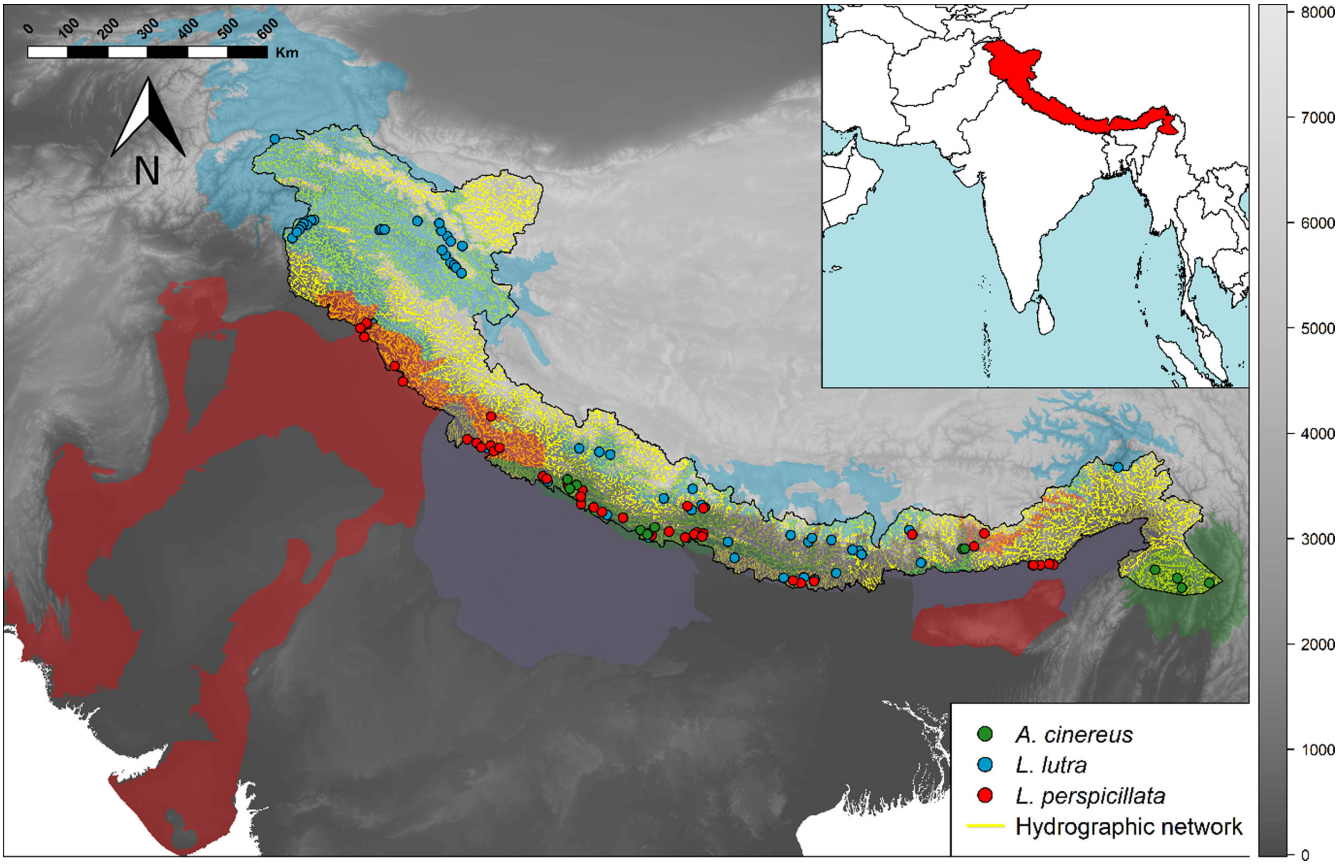


FIGURE 1 Study area, species occurrence data and ecoregions considered for SDMs calibration (green: *A. cinereus*; blue: *L. lutra*; red: *L. perpsicillata*; purple polygons indicate overlapping ecoregions by *A. cinereus* and *L. lutra*). The Digital Elevation Model (grey shadowed) and the hydrographic network (yellow) are reported as background layers

elevation, mean diurnal temperature range, temperature seasonality, precipitation of the driest month, precipitation of the warmest quarter, precipitation of the coldest quarter, diversity of land use categories and Euclidean distance from farmlands, forests, grasslands, urban areas, barren lands and water bodies (Table S1). As specified above, elevation and climate variables were used to calibrate climate SDMs, while the entire predictors set was used for full SDMs.

2.5 | Species distribution models

To calibrate climate and full SDMs, we applied the so-called "ensemble of small models" approach to avoid model overfitting (Breiner et al., 2015), an issue arising when few records are available with respect to the number of predictors (Guisan & Zimmermann, 2000). Accordingly, we trained a set of bivariate models for each species, that is, considering all possible combinations of the environmental covariates taken two at a time (10 combinations per species in climate SDMs and 78 combinations per species in full SDMs), and then averaging each model's results. Bivariate models were calibrated by using two algorithms: generalized linear models (GLMs) and maximum entropy models (Maxent; Phillips et al., 2006). We chose these two algorithms as they reported the highest predictive accuracies within an ensemble of small models context (Breiner et al., 2015, 2018). For each species, we randomly placed a set of 10,000 background points over a region identified by all the WWF Terrestrial Ecoregions (Olson et al., 2001) intersecting the species records gathered in the Himalayan study area (Figure 1; Barve et al., 2011). To evaluate predictive performance of the models, we performed a "block" cross-validation (Muscarella et al., 2014) by splitting data into four geographically non-overlapping bins of equal numbers of occurrences, corresponding to each corner of the entire geographical space. Occurrences falling into three out of four bins were used in turn for model calibration, while the data from the held-out bin were used for evaluation purposes. This method proved useful in assessing model transferability, that is, the ability to extrapolate predictions into new areas/times (Roberts et al., 2017), as well as to penalize models based on biologically meaningless predictors (Fourcade et al., 2018). The predictive performance of each model was assessed by measuring the area under the receiver operating characteristic curve (AUC; Hanley & McNeil, 1982) and the true skill statistic (TSS; Allouche et al., 2006). Models were optimally tuned through an intensive procedure as implemented by Breiner et al. (2018). Specifically, for each bivariate model, we varied parameters and complexity as generated by alternative settings and then chose the configuration that yielded the highest AUC under the block cross-validation scheme (Breiner et al., 2018). For GLMs, we tested the shape of the relationship (i.e., linear, quadratic or cubic) and the interaction level (absent or present). For Maxent, we evaluated regularization values between 0.5

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and 4, with 0.5 steps, and tested the following feature classes: linear, linear + quadratic, hinge, linear + quadratic + hinge, linear + quadratic + hinge + product and linear + quadratic + hinge + product + threshold (Fourcade et al., 2018). The settings configurations that emerged as the optimal ones for most of the tested bivariate models were then used to calibrate final GLMs and Maxent bivariate models (Breiner et al., 2018). Among these, we dropped poorly calibrated models (i.e., achieving AUC <0.7; Di Febbraro et al., 2019) from the subsequent analyses. Ensemble models were obtained by averaging individual GLMs and Maxent models projections weighted by their respective AUC scores (Marmion et al., 2009). For each species, we calculated the relative importance of predictors from the ensemble model using the functionality provided in the "biomod2" package (Thuiller et al., 2009). Lastly, we calculated the spatial autocorrelation in ensemble models residuals through Moran's *I* correlograms (Appendix S4). Differences in predictive performance between climate and full SDMs were assessed through *t*-test.

2.6 | Future scenarios

Climate SDMs were projected on two climate change scenarios (i.e., RCP.26 and RCP.85) from the fifth IPCC assessment (IPCC, 2013). Full SDMs were instead projected on four climate and land use change scenarios obtained by coupling the two abovementioned IPCC scenarios with two land use change scenarios (LUC.B1 and LUC.A2) elaborated by Li et al. (2017; Table S2). As different global circulation models may lead SDMs to predict diverging climate change effects (Buisson et al., 2010), we considered three alternative versions for the RCPs scenarios, yielded by the CCSM4, CNRM-CM5 and MIROC-ESM global circulation models, respectively. The scenarios predict mild (RCP.26 and LUC.B1) to severe (RCP.85 and LUC.A2) alterations in climate and land use in 2050. The corresponding mean temporal trends of the covariates used in the models under all the scenarios are shown in Figure S2. We calculated a multivariate environmental similarity surface (MESS; Elith et al., 2011) to evaluate the effect of model extrapolation on values of predictors lying outside the calibration range (Appendix S5). Current and future SDMs projections were binarized to obtain range maps according to four threshold approaches (i.e., "equalize sensitivity and specificity," "maximize TSS," "mean occurrence probability" and "minimize receiver operating characteristic plot distance"; Liu et al., 2013), as to account for the effect of using different binarization schemes (Di Febbraro et al., 2019).

2.7 | Quantification of the effects of climate and land use change on otter distribution and vulnerability

For each species, model and scenario, we calculated two metrics of climate and land use change effect on binary range maps: net change (in terms of gain/loss percentage) and geographical shift (expressed as 100-percentage overlap between current and future range maps; Franklin et al., 2013). We also assessed the direction of geographical shift by measuring changes in the position of range centroids (Aguirre-Gutiérrez et al., 2016) and margins (Taheri et al., 2021) along longitude, latitude and elevation between current and 2050 range maps (further details are provided in Appendix S6). Species vulnerability to climate and land use change was calculated by following the above mentioned CNFA approach, which was recently implemented by Rinnan and Lawler (2019). This approach relies on ecological niche factor analysis (ENFA, a technique that calculates the environmental niche of a species using presence-only data; Hirzel et al., 2002), to derive two metrics: (i) species sensitivity and (ii) habitat exposure to global change. In particular, sensitivity is calculated as the array of environmental conditions a species tolerates (the so-called specialization vector within the ENFA framework) with respect to a given environmental variable. The rationale behind this metric is that the smaller the range of environmental conditions a species tolerates for a given variable, the smaller its niche width and, consequently, the more sensitive the species will be to strong deviations from these optimal conditions (e.g., under global change; Rinnan & Lawler, 2019). Habitat exposure is calculated as a dissimilarity measure between present and future environmental conditions within a species current habitat: the higher such dissimilarity, the larger the amount of environmental change a species might experience if it remains in place. Species sensitivity and habitat exposure are then combined to calculate vulnerability through the following equation (adapted from Rinnan & Lawler, 2019):

$$v_j = \sqrt{(1 + e_j)s_j}$$

where *s* and *e*, respectively, indicate species sensitivity and habitat exposure to the *j*-th environmental variable. According to the CNFA framework, both sensitivity and exposure were measured within the current distribution of the species (Rinnan & Lawler, 2019). Hence, we alternatively used binary predictions by climate and full SDMs to delineate spatially such current habitat. Specifically, we calculated a different vulnerability value for each binary map deriving from each scenario, global circulation model and binarization threshold. All the vulnerability analyses were carried out using the "CENFA" R package (Rinnan & Lawler, 2019). Differences in vulnerability values between each species pair were assessed through analysis of variance and Tukey post-hoc test. To evaluate the relative contribution of species sensitivity and habitat exposure in determining species vulnerability to climate and land use future scenarios, we regressed vulnerability scores against sensitivity and exposure, respectively, considering each environmental variable. For this purpose, we used linear mixed models (LMM), setting sensitivity and exposure in turn as fixed terms and global circulation model, global change scenario and binarization threshold as random intercepts. LMMs were fitted using the "lme4" R package (Bates et al., 2015).

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3 | RESULTS

3.1 | Species distribution models

Overall, full SDMs significantly outperformed climate SDMs in terms of both AUC ($t = 4.85$, $p < .001$) and TSS ($t = 4.14$, $p < .001$). Specifically, while full SDMs achieved good predictive performances sensu Swets (1988) and Landis and Koch (1977), with AUC values >0.80 and TSS values >0.40 for all species (Table S3), climate SDMs were less accurate, with just one species (i.e., *L. perpsicillata*) reporting an AUC >0.80 and two (i.e., *A. cinereus* and *L. perpsicillata*) achieving TSS values >0.40. In light of that, we hereafter showed and discussed response curves and spatially explicit predictions only for full SDMs (Figure S3–S10). According to these models, both climate and land use variables were listed amongst the most important predictors shaping the distribution of the three species (Figure S4). For example, distance from forests was among the three most contributing predictors for all the species (along with distance from grasslands in *L. lutra*), showing an inverse relationship with their suitability. Moreover, precipitation during the warmest-driest periods was maximally important in *L. perspicillata*, and within the four most important predictors for *A. cinereus* and *L. lutra*, overall indicating moderate precipitation conditions as the most preferred (Figure S4). Elevation was highly important for *L. lutra* (i.e., highest suitability at 1,000–3,500 m asl) and, to a lesser extent, for *A. cinereus* (i.e., suitability peak around 1,000 m asl), while predictors describing temperature fluctuations (i.e., mean diurnal range and temperature seasonality) were among the five most contributing variables for all the three species, showing the otters to prefer a rather high thermal stability (Figure S4). Full SDMs for all the three species exhibited a negligible spatial autocorrelation in their residuals (Appendix S4), as well as a minimal extrapolation effect in models predictions (see Appendix S5 and Figures S7–S9).

3.2 | Quantification of the effects of climate and land use change on otter distribution and vulnerability

Climate SDMs, by accounting for climate change scenarios only, predicted far less severe alterations of otter distribution than full SDMs, which also involve land use change scenarios (Figure 2). Specifically, net change in future distribution as predicted by climate SDMs is clearly negative only for *L. lutra* (median values between −9% and −10%), while it shows far higher values in the other two species, even achieving positive scores (i.e., a net gain in distribution) for *A. cinereus* under RCP.85 scenario, and *L. perspicillata* under RCP.26 scenario (Figure 2). On the contrary, all the three species showed a negative net change in their future distribution under full SDMs, ranging from ca. −6% for *A. cinereus* under RCP.85–LUC.B1 scenario to ca. −15% for *L. lutra* under RCP.85–LUC.A2 (Figures 2 and 3). Similarly, the three species reported lower range shifts under climate SDMs (from ca. 6% for *L. perspicillata* to 14% for *L. lutra*, both under the RCP.26 scenario; Figure 2) than under full SDMs (from ca. 10% for *A. cinereus* under RCP.26–LUC.B1 to 18% for *L. lutra* under RCP.85–LUC.A2; Figures 2 and 3). Overall, the three species exhibited slight to moderate shifts in range centroids towards southeast and lower elevations under most of the scenarios (Appendix S6). Moreover, range margins severely shrank for *A. cinereus* along longitude and latitude, while extending mostly northward for the other two species. Elevation range margins shrank for all the species under almost all scenarios (Appendix S6). In general, scenarios including the most severe land use alterations (i.e., LUC.A2) produced the strongest impact on species distribution, irrespectively of the associated climate change scenario (Figure 2). Such a pattern is particularly evident for *A. cinereus*, where the differences in net change and geographical shift are highest between LUC.B1 and LUC.A2 scenarios and lowest between RCP.26 and RCP.85 scenarios. These differences are less pronounced in the other two species, although LUC.A2 scenarios still hold as the most severe ones (Figure 2). For all the three species, vulnerability values calculated under climate SDMs were largely lower than those computed under full SDMs (Figure 4). Under climate SDMs, *L. lutra* and *A. cinereus* resulted significantly the least and the most vulnerable species to 2050 climate change, whereas *L. perspicillata* showed intermediate vulnerability scores, though always significantly different from those of the other two species (Figure 4; Table S4). Under full SDMs, *L. lutra* achieved significantly lower vulnerability values than both the other two species, while *L. perspicillata* overcame *A. cinereus* as the most vulnerable species, though their vulnerabilities are not significantly different (Figure 4; Table S4). Exactly the same figures apply to species sensitivity scores under the two alternative modelling setups, whereas habitat exposure values are rather similar among the three species (Figure 4). The three otter species also exhibited different patterns in their vulnerability, sensitivity and exposure as partitioned among each climate and land use predictor. Under the worst scenario (i.e., RCP.85–LUC.A2), both *L. lutra* and *L. perspicillata* showed the highest vulnerability to distance from grasslands and forests, though the magnitude of such an effect was far smaller for the first species. *Aonyx cinereus* was moderately vulnerable to temperature seasonality, distance from forests and mean diurnal range (Figures 5, S10). This pattern follows very closely the sensitivity scores exhibited by the three species. In particular, *L. lutra* exhibited a low sensitivity (i.e., wide tolerance) to several variables (Figures 5, S10), emerging as the most generalist species. On the other hand, *L. perspicillata* showed a high sensitivity to distance from grasslands and forests, while *A. cinereus* showed a moderate sensitivity to temperature seasonality and distance from forests (Figure 5). In contrast to sensitivity, the three species exhibited habitat exposure scores of comparable magnitude among each other. In fact, their current habitat is similarly exposed to alterations in mean diurnal range, precipitation of the warmest quarter and distance from grasslands (Figure 5). Taking together the differential contribution of sensitivity and exposure among global circulation models, global change scenarios and binarization thresholds, LMMs outcomes highlighted sensitivity to exert a higher influence than habitat exposure on vulnerability scores. Although statistically significant for all the species, the preponderant role of

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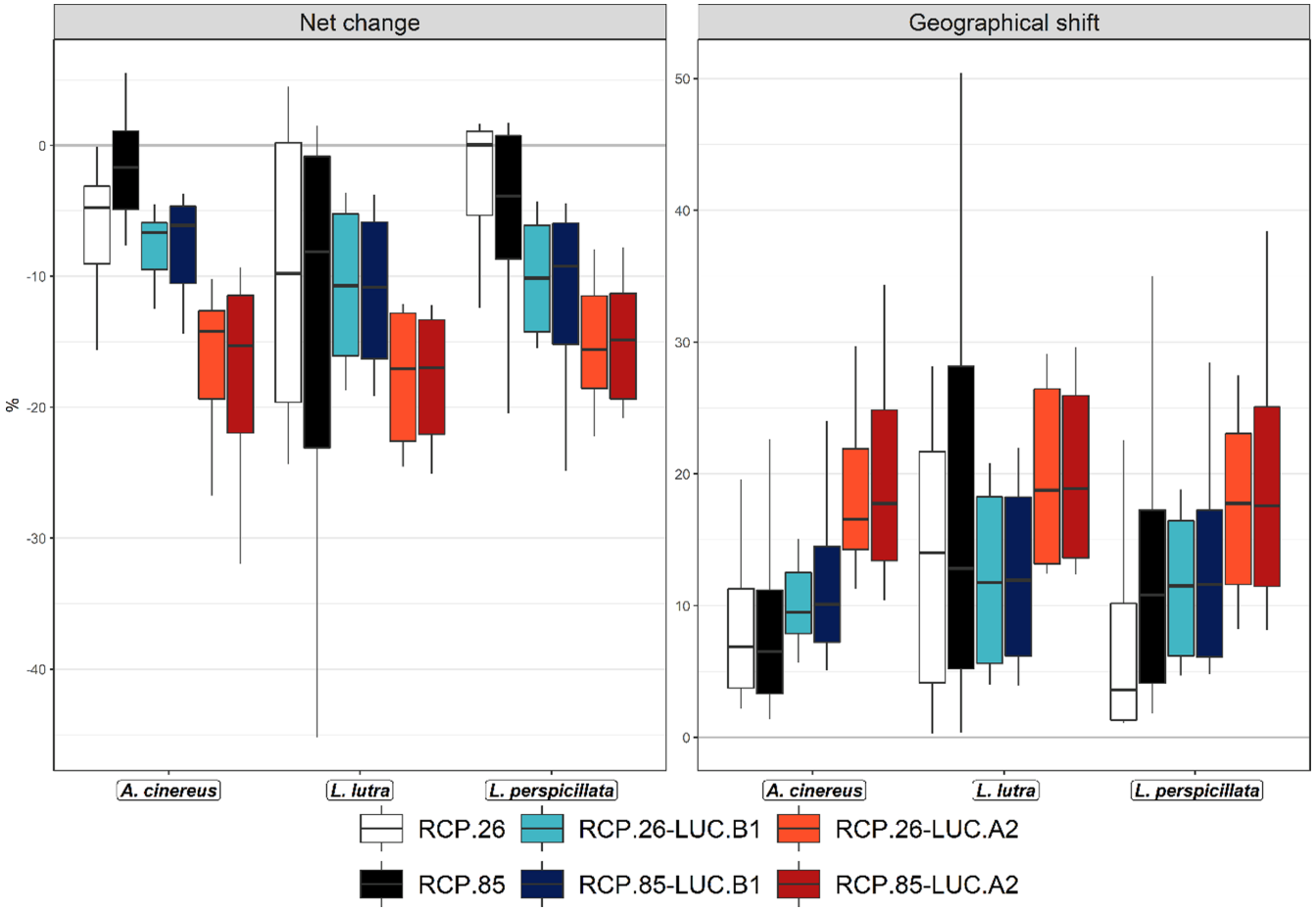


FIGURE 2 Percentage of net area change (on the left) and geographical shift (on the right) in otter distribution under 2050 climate and land use change scenarios. The box plots depict climate change only (i.e., RCP.26 and RCP.85) and combined climate/land use change scenarios, which range from mild (RCP.26-LUC.B1) to severe (RCP.85-LUC.A2) alterations in climate and land use. Models projections are generated by three global circulation models and four binarization thresholds. Black/white colours indicate climate change only scenarios, while blue (red) colour tones refer to low- (high-) severity land use change scenarios. In the box plots, the central line represents the median, while the box comprises the interquartile range (IQR). The upper whisker represents the 3rd quartile +1.5 IQR while the lower whisker is 1st quartile−1.5 IQR

sensitivity emerged most clearly for *L. perspicillata* (Figure 6). On the other hand, the statistical relationship between habitat exposure and vulnerability is overall weaker, and not even significant for *L. perspicillata* (Figure 6).

4 | DISCUSSION

According to our results, future climate and land use change will exert an overall detrimental effect on the geographical range of the three otter species in the Himalaya, contributing to high vulnerability values. In particular, all the three species will undergo moderate to severe shrinking and shift in their distribution under 2050 global change scenarios, especially as predicted by models accounting for both climate and land use future alterations. In fact, amongst the global change scenarios considered in our assessment, land use modifications are predicted to exert the most severe effects on all the three species irrespectively of the associated climate change scenario. Our results allowed us to confirm both the initial hypotheses, reporting far higher vulnerability scores to 2050 global change when including both climate and land use drivers (hypothesis i), as well as a significantly preponderant effect of niche width rather than habitat exposure (which is overall high and similar among the species) in determining vulnerability values (hypothesis ii). In keeping with that, the most specialist species, *L. perspicillata*, showed the highest vulnerability as opposed to the most generalist, least vulnerable species, *L. lutra*.

The potential distribution of the three otter species is overall shaped by a mixture of climate and land use variables. For instance, *A. cinereus* and *L. perspicillata* showed similar environmental preferences, reporting the highest suitability in forest habitats with moderate precipitation during the warmest season. Such outcomes are in keeping with the well-known preference of the two species for moist forests (e.g., mangrove or peat swamp forests; Duplaix & Savage, 2018; Foster-Turley, 1992; Gupta et al., 2020). Moreover, *L. perspicillata* and *A. cinereus*, respectively,

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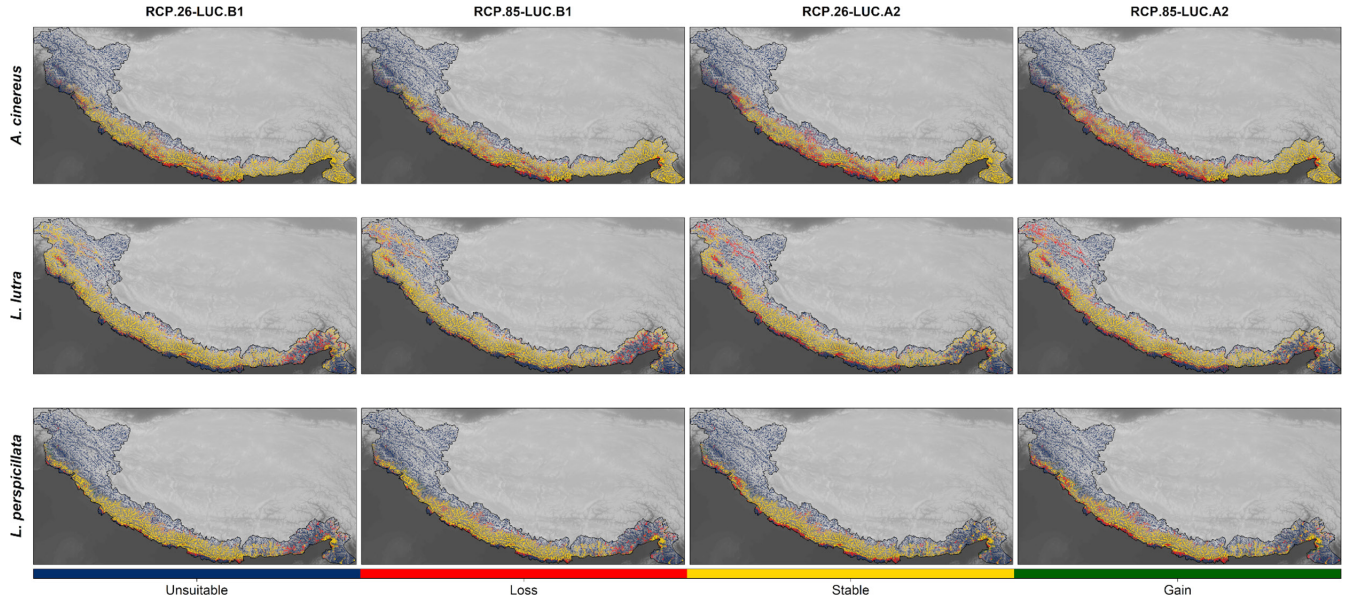


FIGURE 3 Spatially explicit predictions of otter range modifications under 2050 climate and land use change scenarios, as generated by the MIROC-ESM global circulation model and the "maximize TSS" binarization threshold. Blue: stable unsuitable habitat, red: habitat loss, yellow: stable suitable habitat, green: habitat gain

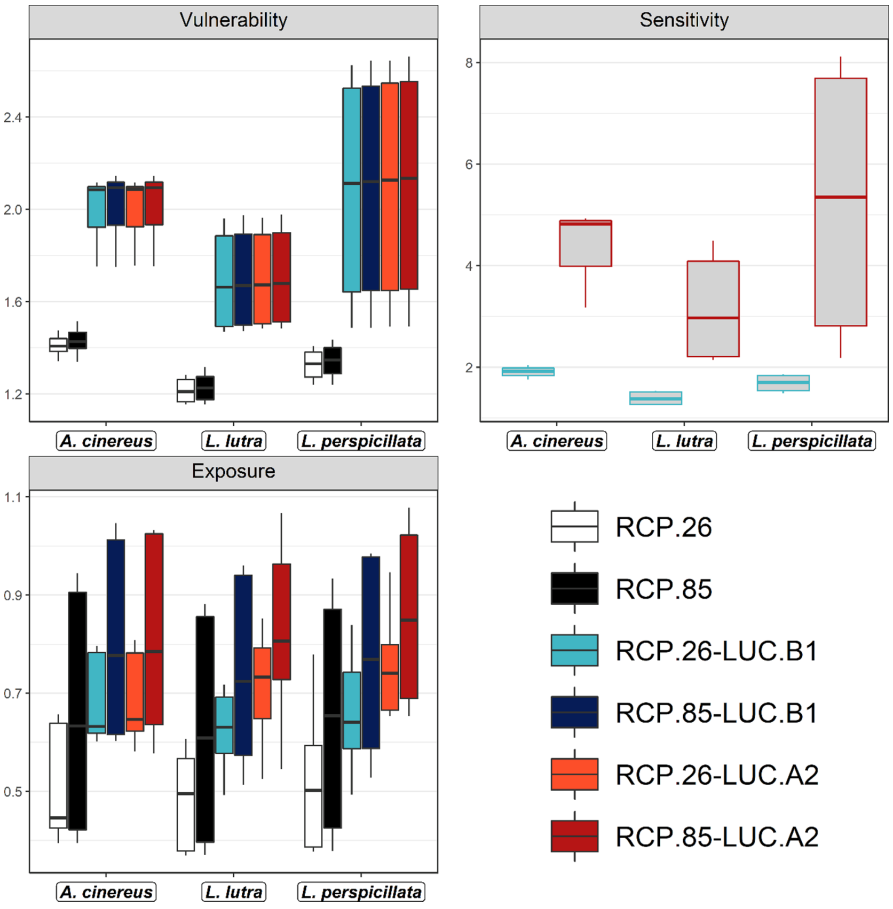


FIGURE 4 Otter total vulnerability, along with species sensitivity and habitat exposure to the six 2050 climate and land use change scenarios, as generated by three global circulation models and four binarization thresholds. Box plots colours for vulnerability and exposure panels refer to climate change only (i.e., black and white) and combined climate and land use change scenarios (from blue to red tones), while border colours in box plots for sensitivity refer to such metric calculated on climate and topographic variables only (cyan; as done under climate SDMs) and on the entire predictors set (dark red; as done under full SDMs)

feed on fish and invertebrates (i.e., crustaceans and shellfish; Anoop & Hussain, 2005; Duplaix & Savage, 2018; Foster-Turley & Markowitz, 1982; Kanchanasaka & Duplaix, 2011), whose abundance in freshwater streams can be altered by scarce (i.e., drought) or extreme (i.e., floods) rainfall regimes (Chea et al., 2020; Gratwicke, 2004; Milner et al., 2013). This evidence further confirms

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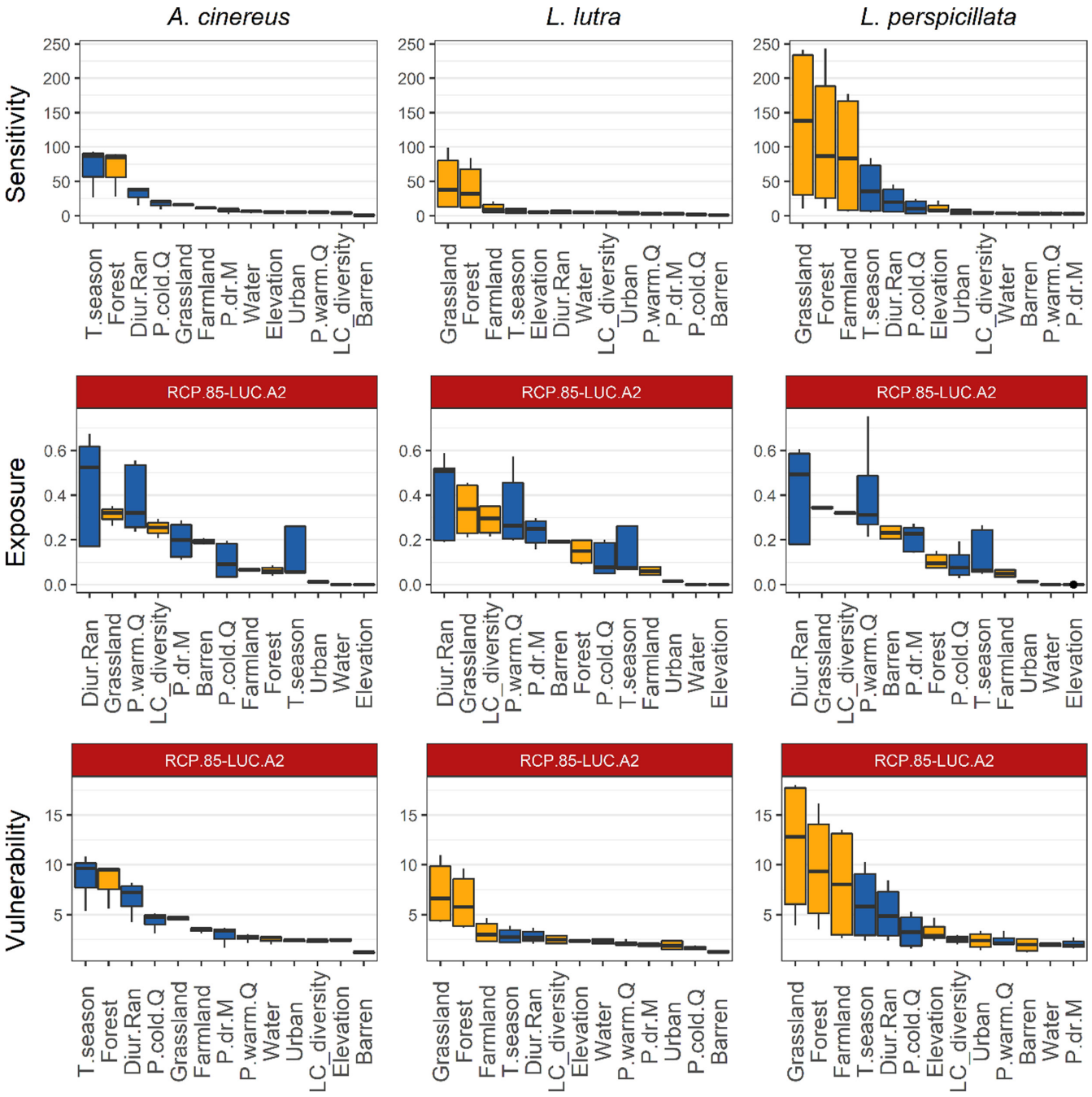


FIGURE 5 Species sensitivity, habitat exposure and vulnerability to 2050 worst scenario (i.e., RCP.85-LUCA2) calculated for each climate and land use predictor. Box plots include results generated by three global circulation models and four binarization thresholds. Land use variables are depicted in gold, while climate variables are shown in blue. Variables complete names and descriptions are provided in Table S1

the importance of precipitation-related variables in shaping the distribution of these two species. Particularly for *A. cinereus*, we also predicted a marked effect of temperature fluctuations, as indicated by the high importance scores of seasonality. Although with a lower magnitude, this outcome is apparent also for *L. perspicillata*, where mean diurnal range and temperature seasonality emerged among the most important predictors. In fact, the two species shows the highest suitability in overall thermally stable habitats. This pattern partly recalls the evidence provided by Cianfrani et al. (2018), which showed *A. cinereus*, and to a lesser extent also *L. perspicillata*, to be affected by temperature fluctuations, although mostly in terms of thermal diurnal range. Grassland and forest habitats with moderate precipitation during the driest month emerged as the most preferred environments by *L. lutra*. These outcomes are largely consistent with previous investigations of this species. For instance, the role of herbaceous and forested habitats as resting and reproduction sites for *L. lutra* also emerged in Cianfrani et al. (2010), in keeping with previous similar evidence (e.g., Beja, 1996; Prenda &

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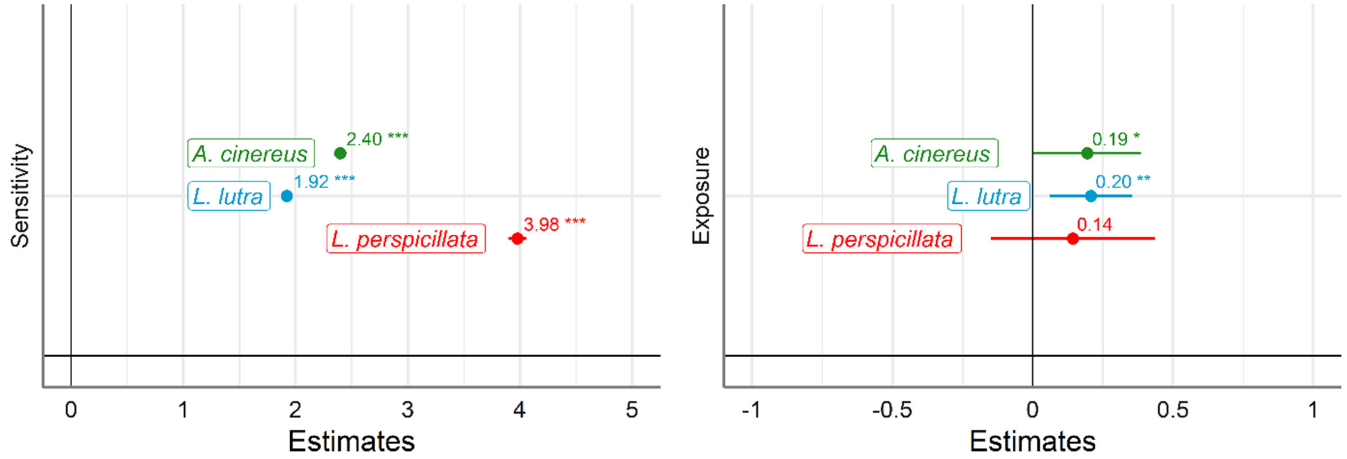


FIGURE 6 Estimates and statistical significance of the coefficients in the linear mixed models fitted between otter vulnerability and sensitivity or exposure, in turn (*p* value legend: *, <0.05; **, <0.01; ***, <0.001)

Granado-Lorencio, 1996; Prenda et al., 2001). Moreover, Cianfrani et al. (2011, 2018) carried out modelling studies reporting precipitation during the driest month among the most important drivers affecting *L. lutra* geographical distribution. The relevance of this predictor is likely linked to its effects on hydrological regimes and river characteristics, which in turn affect *L. lutra* habitat availability, especially during the dry season (Kruuk, 2006; Scorpio et al., 2016). Overall, elevation also contributed to shape otter distribution, especially for *L. lutra*. While this species exhibited moderate to high suitability values along a wide altitudinal gradient, confirming its environmental flexibility (Kruuk, 2006; Remonti et al., 2009), *A. cinereus* suitability sharply decreased toward high elevations (Duplaix & Savage, 2018), although we cannot entirely exclude such pattern to be altered by a lower sampling effort at higher elevation, or by competitive exclusion possibly exerted by *L. lutra*. Raha and Hussain (2016), exploring the habitat use of the three species in Western Ghats (i.e., a tropical plain and mountain area in southwestern India), found *L. perspicillata* and *L. lutra* to prefer dense forested areas at low to intermediate elevations, while *A. cinereus* tends to occur in waterbodies at higher elevations surrounded by dense grassland. In fact, such evidence is only partly coherent with our findings, though it is important to remark that our study context (i.e., the Himalayan chain) is far different from the area investigated by Raha and Hussain (2016). In addition, such partial inconsistencies may depend upon the great variability of habitat types the three species are known to use throughout their range (Duplaix & Savage, 2018).

Interestingly, our predictions showed land use change to remarkably override the future role played by climate change. In fact, A2 land use change scenario was systematically associated with the severest range contraction and shift in all the three species, whether in combination with low- or high-intensity climate change scenarios. Under A2 scenarios, Himalayan landscape will increase farmlands and more urbanized areas in lieu of forests and grasslands (Figure S2), therefore impacting two of the most important land use categories driving otter distribution (Figure S4). Despite a noticeable scarcity of studies designed to forecast both climate and land use change impacts on species distribution (Titeux et al., 2017), a pattern where land use change effects overtake those by climate change has been observed several times (Sirami et al., 2017). For instance, Eglington and Pearce-Higgins (2012) pointed out how long-term trends in UK bird populations have been predominantly affected by alterations in land use intensity rather than by climate change. An even stronger divergence between the effects of these two global change drivers was showed by Di Febbraro et al. (2019), which predicted future climate change to ease invasion risk by alien squirrels as opposed to the strongly detrimental effect played by land use alterations. The importance of considering both climate and land use in predictive studies on biodiversity has been repeatedly underlined (Sirami et al., 2017; Titeux et al., 2017), though it started to be adequately accounted for only in rather recent times (Newbold, 2018; Peters et al., 2019). It is well-established that modelling species response to climate change only may provide substantially different predictions compared to those including land use change as well, thus hampering adequate conservation recommendations (Di Febbraro et al., 2019; Sirami et al., 2017). This evidence substantially explains why the outcomes from full SDMs are largely divergent (and overall more accurate) from those yielded by climate SDMs, as well as by other studies that analysed otter future distribution exclusively under climate change scenarios. For instance, Cianfrani et al. (2018) predicted a loss in global suitable area of −5% to −20% for *L. perspicillata*. While such prediction largely coincides with our results under climate SDMs, we reported a severer loss (−7% to −25%) under high-intensity land use change scenarios. Even, Cianfrani et al. (2018) showed an overall increase in suitable area under climate change for *L. lutra* (+10% to +11%), whereas we predicted a systematical loss for this species, especially under the high-intensity land use change scenarios. That said, we cannot exclude that such inconsistencies may partly depend on the different geographical extent adopted in Cianfrani et al. (2018; i.e., global scale) with respect to our study setup. It is also noteworthy that we focused on the Himalayan region, which encompasses the margins of the altitudinal ranges of the three species. Accordingly, resident otters might present local

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adaptations to mountain environments, thus likely being more susceptible to climate and land use alterations if compared to lowland populations. This pattern seems particularly plausible for *L. lutra*, whose several subspecies are distributed in discrete spatial enclaves, especially along the Himalaya (Hung & Law, 2016). In fact, a solid body of literature has shown that there can be important geographical intraspecific variation in the sensitivity and response to changing environmental conditions (Nice et al., 2019; Peterson et al., 2019). Such intraspecific variation in environmental requirements substantially derives from local adaptation or adaptive plasticity along the gradient of environmental conditions (Macdonald et al., 2018). Consequently, predictions of species response to global change that neglect to account for such intraspecific differences may strongly diverge from those generated from local partitions of species distributions (Martin et al., 2020). This evidence could further explain the difference between our predictions of otter future distribution and those provided by Cianfrani et al. (2018).

The evaluation of otter vulnerability determinants showed species sensitivity to play the most important contribution, whereas habitat exposure effect was mostly negligible for all the three species. This pattern emerges even more clearly by looking at how the three species are ranked according to sensitivity, exposure and vulnerability. Despite reporting intermediate to high exposure values, *L. lutra* was ranked as the least vulnerable species, by virtue of its lowest sensitivity. Analogously, *A. cinereus* scored a median vulnerability ca. 30% higher than *L. lutra*, though these two species showed largely similar exposure values. Such outcomes confirm well-documented evidence that habitat exposure, while being the most used metric in vulnerability assessments (Foden et al., 2019), is not necessarily consistent with niche measures of species intrinsic sensitivity (Dickinson et al., 2014). This tendency was also highlighted for otters within the global scale vulnerability assessment performed by Cianfrani et al. (2018). As for the three species we focused on, such assessment reported *L. lutra* and *L. perspicillata* as the least and the most vulnerable species, respectively. Interestingly, although Cianfrani et al. (2018) showed a higher exposure for *A. cinereus* than for *L. perspicillata* (in contrast to our results), the latter was consistently more vulnerable by virtue of a far higher sensitivity. This body of evidence substantially emphasizes the importance of assessing vulnerability by including trait-based elements, for example, measures of niche width, into "classical" correlative approaches usually adopted to predict range dynamics (Foden et al., 2019; Pacifici et al., 2015).

As for the main limitations of this study, we did not consider the third component usually included in the CCVA theoretical framework, that is, the adaptive capacity (Foden et al., 2019). Such ability to adjust to environmental change should be inferred by traits as for example, phenotypic plasticity or dispersal abilities, which are often unavailable for many species. This lack of information makes adaptive capacity the most challenging component to be quantified in CCVAs, which often simply neglect it (Cianfrani et al., 2018; Foden et al., 2019). It is worth mentioning that species sensitivity and habitat exposure can be given different weights as to tune their relative contribution to the final vulnerability score (Rinnan & Lawler, 2019). Although the way such weights are defined should bias, at least in theory, the vulnerability score toward sensitivity or exposure, Cianfrani et al. (2018) designed a specific analysis showing that different weighting schemes on the single vulnerability components altered the final score only marginally (especially for the three species analysed here). Furthermore, we were interested in quantifying the relative contribution of sensitivity and exposure on vulnerability accounting for several variability sources (e.g., global circulation models, global change scenarios and binarization thresholds). Accordingly, we found the most obvious choice was to assign the same weight (i.e., 1) to both vulnerability components, instead of artificially introducing any weighting scheme that lacked of a strong ecological rationale. Lastly, we did not include any projection of climatic extreme events (e.g., drought or floods) in our vulnerability assessment. Despite a well-established evidence that such events will likely have stronger effects on ecological systems than simple shifts in mean values (Thompson et al., 2013), modelling their frequency and occurrence is particularly difficult due to their rarity and stochastic nature. As a result, such phenomena have usually been neglected in conservation studies until very recently (Palmer et al., 2017).

5 | CONCLUSIONS

Notwithstanding these drawbacks, our study underlines how coupling climate and land use change in CCVAs can generate profoundly diverging results compared to approaches relying on solely climate change. Such ever-mounting evidence appears particularly relevant both to reassess more cautionarily the species ranked as insensitive or favoured by climate change (e.g., *L. lutra*), and, even more, to increase attention on those species (e.g., African otters *A. congicus* and *A. capensis*) that were already classified as highly vulnerable under climate change scenarios only (Cianfrani et al., 2018). The outcomes of this study also highlight the potentialities of performing CCVAs through a "combined" framework, thus emphasizing the importance of including trait-based elements (e.g., species sensitivity) into purely correlative approaches (Foden et al., 2019; Pacifici et al., 2015). In fact, such intrinsic elements proved significantly more important in determining species vulnerability than extrinsic metrics such as habitat exposure. Our analyses show that such a pattern still holds when accounting for several variability sources usually linked to correlative models (e.g., alternative global circulation models and binarization schemes). Future research efforts should focus on developing tools to quantify adaptive capacity in a more reliable and generalizable way than currently available approaches (Williams et al., 2008). Including this "great absent" in CCVAs, along with a deeper focus on modelling climate variability and extreme events, will surely bring this conservation tool towards a more advanced level.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.zw3r2287v.

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REFERENCES

Aguirre-Gutiérrez, J., Kissling, W. D., Carvalheiro, L. G., WallisDevries, M. F., Franzén, M., & Biesmeijer, J. C. (2016). Functional traits help to explain half-century long shifts in pollinator distributions. *Scientific Reports*, *6*(1), 1–13. https://doi.org/10.1038/srep24451

Allouche, O., Tsoar, A., & Kadmon, R. (2006). Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, *43*(6), 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x

Anoop, K. R., & Hussain, S. A. (2005). Food and feeding habits of smooth-coated otters (*Lutra perspicillata*) and their significance to the fish population of Kerala, India. *Journal of Zoology*, *266*(1), 15–23. https://doi.org/10.1017/S0952836905006540

Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S. P., Peterson, A. T., Soberón, J., & Villalobos, F. (2011). The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecological Modelling*, *222*(11), 1810–1819. https://doi.org/10.1016/j.ecolmodel.2011.02.011

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Beja, P. R. (1996). Temporal and spatial patterns of rest-site use by four female otters *Lutra lutra* along the south-west coast of Portugal. *Journal of Zoology*, *239*(4), 741–753. https://doi.org/10.1111/j.1469-7998.1996.tb05475.x

Beniston, M. (2003). Climatic change in Mountain regions: A review of possible impacts. In H. Diaz (Ed.), *Climate variability and change in high elevation regions: Past, present & future* (pp. 5–31). Springer.

Borges, F. J. A., Ribeiro, B. R., Lopes, L. E., & Loyola, R. (2019). Bird vulnerability to climate and land use changes in the Brazilian Cerrado. *Biological Conservation*, *236*, 347–355. https://doi.org/10.1016/j.biocon.2019.05.055

Breiner, F. T., Guisan, A., Bergamini, A., & Nobis, M. P. (2015). Overcoming limitations of modelling rare species by using ensembles of small models. *Methods in Ecology and Evolution*, *6*(10), 1210–1218. https://doi.org/10.1111/2041-210X.12403

Breiner, F. T., Nobis, M. P., Bergamini, A., & Guisan, A. (2018). Optimizing ensembles of small models for predicting the distribution of species with few occurrences. *Methods in Ecology and Evolution*, *9*(4), 802–808. https://doi.org/10.1111/2041-210X.12957

Brook, B. W., Sodhi, N. S., & Bradshaw, C. J. A. (2008). Synergies among extinction drivers under global change. *Trends in Ecology & Evolution*, *23*(8), 453–460. https://doi.org/10.1016/J.TREE.2008.03.011

Buisson, L., Thuiller, W., Casajus, N., Lek, S., & Grenouillet, G. (2010). Uncertainty in ensemble forecasting of species distribution. *Global Change Biology*, *16*(4), 1145–1157. https://doi.org/10.1111/j.1365-2486.2009.02000.x

Chakraborty, A., Joshi, P. K., & Sachdeva, K. (2018). Capturing forest dependency in the central Himalayan region: Variations between Oak (*Quercus* spp.) and Pine (*Pinus* spp.) dominated forest landscapes. *Ambio*, *47*(4), 504–522. https://doi.org/10.1007/s13280-017-0947-1

Chea, R., Pool, T. K., Chevalier, M., Ngor, P., So, N., Winemiller, K. O., Lek, S., & Grenouillet, G. (2020). Impact of seasonal hydrological variation on tropical fish assemblages: Abrupt shift following an extreme flood event. *Ecosphere*, *11*(12), e03303. https://doi.org/10.1002/ecs2.3303

Chen, F., Wang, J., Jin, L., Zhang, Q., Li, J., & Chen, J. (2009). Rapid warming in mid-latitude central Asia for the past 100 years. *Frontiers of Earth Science in China*, *3*(1), 42–50. https://doi.org/10.1007/s11707-009-0013-9

Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, *333*(6045), 1024–1026. https://doi.org/10.1126/science.1206432

Cianfrani, C., Broennimann, O., Loy, A., & Guisan, A. (2018). More than range exposure: Global otter vulnerability to climate change. *Biological Conservation*, *221*, 103–113. https://doi.org/10.1016/j.biocon.2018.02.031

Cianfrani, C., Lay, G. L., Maiorano, L., Satizábal, H. F., Loy, A., & Guisan, A. (2011). Adapting global conservation strategies to climate change at the European scale: The otter as a flagship species. *Biological Conservation*, *144*(8), 2068–2080. https://doi.org/10.1016/j.biocon.2011.03.027

Cianfrani, C., Le Lay, G., Hirzel, A. H., & Loy, A. (2010). Do habitat suitability models reliably predict the recovery areas of threatened species? *Journal of Applied Ecology*, *47*(2), 421–430. https://doi.org/10.1111/j.1365-2664.2010.01781.x

Di Febbraro, M., Menchetti, M., Russo, D., Ancillotto, L., Aloise, G., Roscioni, F., Preatoni, D. G., Loy, A., Martinoli, A., Bertolino, S., & Mori, E. (2019). Integrating climate and land-use change scenarios in modelling the future spread of invasive squirrels in Italy. *Diversity and Distributions*, *25*(4), 644–659. https://doi.org/10.1111/ddi.12890

Dickinson, M. G., Orme, C. D. L., Suttle, K. B., & Mace, G. M. (2014). Separating sensitivity from exposure in assessing extinction risk from climate change. *Scientific Reports*, *4*(1), 6898. https://doi.org/10.1038/srep06898

Duplaix, N., & Savage, M. (2018). *The global otter conservation strategy*. Salem, Oregon, USA: IUCN/SSC Otter Specialist Group.

Eglington, S. M., & Pearce-Higgins, J. W. (2012). Disentangling the relative importance of changes in climate and land-use intensity in driving recent bird population trends. *PLoS One*, *7*(3), e30407. https://doi.org/10.1371/journal.pone.0030407

Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E., & Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, *17*(1), 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x

Foden, W. B., Young, B. E., Akçakaya, H. R., Garcia, R. A., Hoffmann, A. A., Stein, B. A., Thomas, C. D., Wheatley, C. J., Bickford, D., Carr, J. A., Hole, D. G., Martin, T. G., Pacifici, M., Pearce-Higgins, J. W., Platts, P. J., Visconti, P., Watson, J. E. M., & Huntley, B. (2019). Climate change vulnerability assessment of species. *Wiley Interdisciplinary Reviews: Climate Change*, *10*(1), 1–36. https://doi.org/10.1002/wcc.551

Foster-Turley, P. A. (1992). Conservation aspects of the ecology of Asian small- clawed and smooth Otters on the Malay Peninsula. *IUCN Otter Specialist Group Bulletin*, *7*, 26–29.

Foster-Turley, P., & Markowitz, H. (1982). A captive behavioral enrichment study with Asian small-clawed river otters (*Aonyx cinerea*). *Zoo Biology*, *1*(1), 29–43. https://doi.org/10.1002/zoo.1430010104

Fourcade, Y., Besnard, A. G., & Secondi, J. (2018). Paintings predict the distribution of species, or the challenge of selecting environmental predictors and evaluation statistics. *Global Ecology and Biogeography*, *27*(2), 245–256. https://doi.org/10.1111/geb.12684

Franklin, J., Davis, F. W., Ikegami, M., Syphard, A. D., Flint, L. E., Flint, A. L., & Hannah, L. (2013). Modeling plant species distributions under

14724642, 2022, 8, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ddi.13377, Wiley Online Library on [23/09/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

future climates: How fine scale do climate projections need to be? *Global Change Biology*, *19*(2), 473–483. https://doi.org/10.1111/gcb.12051

Garcia, R. A., Araújo, M. B., Burgess, N. D., Foden, W. B., Gutsche, A., Rahbek, C., & Cabeza, M. (2014). Matching species traits to projected threats and opportunities from climate change. *Journal of Biogeography*, *41*(4), 724–735. https://doi.org/10.1111/jbi.12257

Gratwicke, B. (2004). Migration of the freshwater crab Potamonautes unispinus in a seasonal stream, Zimbabwe. *African Zoology*, *39*(1), 25–29.

Guisan, A., & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling*, *135*(2–3), 147–186. https://doi.org/10.1016/S0304-3800(00)00354-9

Gupta, N., Tiwari, V., Everard, M., Savage, M., Hussain, S. A., Chadwick, M. A., Johnson, J. A., Nawab, A., & Belwal, V. K. (2020). Assessing the distribution pattern of otters in four rivers of the Indian Himalayan biodiversity hotspot. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *30*(3), 601–610. https://doi.org/10.1002/aqc.3284

Guzha, A. C., Rufino, M. C., Okoth, S., Jacobs, S., & Nóbrega, R. L. B. (2018). Impacts of land use and land cover change on surface runoff, discharge and low flows: Evidence from East Africa. *Journal of Hydrology: Regional Studies*, *15*, 49–67. https://doi.org/10.1016/J.EJRH.2017.11.005

Hanley, J. A., & McNeil, B. J. (1982). The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology*, *143*(1), 29–36. https://doi.org/10.1148/radiology.143.1.7063747

Hirzel, A., Hausser, J., Chessel, D., & Perrin, N. (2002). Ecological-niche factor analysis: How to compute habitat-suitability maps without absence data? *Ecology*, *83*(7), 2027–2036. https://doi.org/10.1890/0012-9658(2002)083[2027:ENFAHT]2.0.CO;2

Hung, N., & Law, C. J. (2016). *Lutra lutra* (Carnivora: Mustelidae). *Mammalian Species*, *48*(940), 109–122. https://doi.org/10.1093/mspecies/sew011

IPCC (2013). Climate Change 2013: The Physical Science Basis. In T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, & P. M. Midgley (Eds.), *Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 1535). Cambridge University Press.

Jarvis, A., Reuter, H. I., Nelson, A., & Guevara, E. (2008). *Hole-filled SRTM for the globe Version 4*. Available from the CGIAR-CSI SRTM 90m Database. http://srtm.csi.cgiar.org

Kanchanasaka, B., & Duplaix, N. (2011). Food Habits of the Hairy-nosed otter (*Lutra sumatrana*) and the Small-clawed otter (*Aonyx cinereus*) in Pru Toa Daeng Peat Swamp Forest, Southern Thailand. *Proceedings of Xth International Otter Colloquium, IUCN Otter Spec. Group Bulletin*, *28*(A), 139–161.

Kiruki, H. M., Zanden, E. H., Malek, Ž., & Verburg, P. H. (2017). Land cover change and woodland degradation in a charcoal producing semi-arid area in Kenya. *Land Degradation & Development*, *28*(2), 472–481. https://doi.org/10.1002/ldr.2545

Kruuk, H. (2006). *Otters: Ecology, behaviour and conservation*. Oxford University Press.

Lambin, E. F. (1999). Monitoring forest degradation in tropical regions by remote sensing: Some methodological issues. *Global Ecology and Biogeography*, *8*(3–4), 191–198. https://doi.org/10.1046/j.1365-2699.1999.00123.x

Landis, J. R., & Koch, G. G. (1977). The measurement of observer agreement for categorical data. *Biometrics*, *33*, 159–174. https://doi.org/10.2307/2529310

Leadley, P. (2010). *Biodiversity scenarios: projections of 21st century change in biodiversity, and associated ecosystem services: a technical report for the global biodiversity outlook 3* (Issue 50). UNEP/Earthprint.

Lehner, B., Verdin, K., & Jarvis, A. (2008). New global hydrography derived from spaceborne elevation data. *Eos*, *89*(10), 93–94. https://doi.org/10.1029/2008EO100001

Li, X., Chen, G., Liu, X., Liang, X., Wang, S., Chen, Y., Pei, F., & Xu, X. (2017). A new global land-use and land-cover change product at a 1-km resolution for 2010 to 2100 based on human-environment interactions. *Annals of the American Association of Geographers*, *107*(5), 1040–1059. https://doi.org/10.1080/24694452.2017.1303357

Liu, C., White, M., & Newell, G. (2013). Selecting thresholds for the prediction of species occurrence with presence-only data. *Journal of Biogeography*, *40*(4), 778–789. https://doi.org/10.1111/jbi.12058

Macdonald, S. L., Llewelyn, J., & Phillips, B. L. (2018). Using connectivity to identify climatic drivers of local adaptation. *Ecology Letters*, *21*(2), 207–216. https://doi.org/10.1111/ele.12883

Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R. K., & Thuiller, W. (2009). Evaluation of consensus methods in predictive species distribution modelling. *Diversity and Distributions*, *15*(1), 59–69. https://doi.org/10.1111/j.1472-4642.2008.00491.x

Martin, Y., Van Dyck, H., Legendre, P., Settele, J., Schweiger, O., Harpke, A., Wiemers, M., Ameztegui, A., & Titeux, N. (2020). A novel tool to assess the effect of intraspecific spatial niche variation on species distribution shifts under climate change. *Global Ecology and Biogeography*, *29*(3), 590–602. https://doi.org/10.1111/geb.13036

Milner, A. M., Robertson, A. L., McDermott, M. J., Klaar, M. J., & Brown, L. E. (2013). Major flood disturbance alters river ecosystem evolution. *Nature Climate Change*, *3*(2), 137–141. https://doi.org/10.1038/nclimate1665

Muscarella, R., Galante, P. J., Soley-Guardia, M., Boria, R. A., Kass, J. M., Uriarte, M., & Anderson, R. P. (2014). ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. *Methods in Ecology and Evolution*, *5*(11), 1198–1205. https://doi.org/10.1111/2041-210X.12261

Newbold, T. (2018). Future effects of climate and land-use change on terrestrial vertebrate community diversity under different scenarios. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1881), 20180792. https://doi.org/10.1098/rspb.2018.0792

Nice, C. C., Forister, M. L., Harrison, J. G., Gompert, Z., Fordyce, J. A., Thorne, J. H., Waetjen, D. P., & Shapiro, A. M. (2019). Extreme heterogeneity of population response to climatic variation and the limits of prediction. *Global Change Biology*, *25*(6), 2127–2136. https://doi.org/10.1111/gcb.14593

Oliver, T. H., Isaac, N. J. B., August, T. A., Woodcock, B. A., Roy, D. B., & Bullock, J. M. (2015). Declining resilience of ecosystem functions under biodiversity loss. *Nature Communications*, *6*(1), 1–8. https://doi.org/10.1038/ncomms10122

Oliver, T. H., & Morecroft, M. D. (2014). Interactions between climate change and land use change on biodiversity: Attribution problems, risks, and opportunities. *Wiley Interdisciplinary Reviews: Climate Change*, *5*(3), 317–335. https://doi.org/10.1002/wcc.271

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., Damico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P., & Kassem, K. R. (2001). Terrestrial Ecoregions of the World: A new map of life on Earth. *BioScience*, *51*(11), 933. https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Pacifici, M., Foden, W. B., Visconti, P., Watson, J. E. M., Butchart, S. H. M., Kovacs, K. M., Scheffers, B. R., Hole, D. G., Martin, T. G., Akçakaya, H. R., Corlett, R. T., Huntley, B., Bickford, D., Carr, J. A., Hoffmann, A. A., Midgley, G. F., Pearce-Kelly, P., Pearson, R. G., Williams, S. E., … Rondinini, C. (2015). Assessing species vulnerability to climate change. *Nature Climate Change*, *5*(3), 215–225. https://doi.org/10.1038/nclimate2448

Palmer, G., Platts, P. J., Brereton, T., Chapman, J. W., Dytham, C., Fox, R., Pearce-Higgins, J. W., Roy, D. B., Hill, J. K., & Thomas, C. D. (2017). Climate change, climatic variation and extreme biological responses. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1723), 20160144. https://doi.org/10.1098/rstb.2016.0144

Pereira, H. M., Navarro, L. M., & Martins, I. S. (2012). Global biodiversity change: The bad, the good, and the unknown. *Annual Review*

14724642, 2022, 8, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ddi.13377, Wiley Online Library on [23/09/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

of Environment and Resources, *37*. https://doi.org/10.1146/annurev-environ-042911-093511

Peters, M. K., Hemp, A., Appelhans, T., Becker, J. N., Behler, C., Classen, A., Detsch, F., Ensslin, A., Ferger, S. W., Frederiksen, S. B., Gebert, F., Gerschlauer, F., Gütlein, A., Helbig-Bonitz, M., Hemp, C., Kindeketa, W. J., Kühnel, A., Mayr, A. V., Mwangomo, E., … Steffan-Dewenter, I. (2019). Climate–land-use interactions shape tropical mountain biodiversity and ecosystem functions. *Nature*, *568*(7750), 88–92. https://doi.org/10.1038/s41586-019-1048-z

Peterson, M. L., Doak, D. F., & Morris, W. F. (2019). Incorporating local adaptation into forecasts of species' distribution and abundance under climate change. *Global Change Biology*, *25*(3), 775–793. https://doi.org/10.1111/gcb.14562

Phillips, S. S. J., Anderson, R. P. R., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, *190*(3–4), 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Prenda, J., & Granado-Lorencio, C. (1996). The relative influence of riparian habitat structure and fish availability on otter *Lutra lutra* L. sprainting activity in a small mediterranean catchment. *Biological Conservation*, *76*(1), 9–15. https://doi.org/10.1016/0006-3207(95)00080-1

Prenda, J., Lpez-Nieves, P., & Bravo, R. (2001). Conservation of otter (Lutra lutra) in a Mediterranean area: The importance of habitat quality and temporal variation in water availability. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *11*(5), 343–355. https://doi.org/10.1002/aqc.454

Raha, A., & Hussain, S. A. (2016). Factors affecting habitat selection by three sympatric otter species in the southern Western Ghats, India. *Acta Ecologica Sinica*, *36*(1), 45–49. https://doi.org/10.1016/j.chnaes.2015.12.002

Remonti, L., Balestrieri, A., & Prigioni, C. (2009). Altitudinal gradient of Eurasian otter (*Lutra lutra*) food niche in Mediterranean habitats. *Canadian Journal of Zoology*, *87*(4), 285–291. https://doi.org/10.1139/Z09-011

Rinnan, D. S., & Lawler, J. (2019). Climate-niche factor analysis: A spatial approach to quantifying species vulnerability to climate change. *Ecography*, *42*(9), 1494–1503. https://doi.org/10.1111/ecog.03937

Roberts, D. R., Bahn, V., Ciuti, S., Boyce, M. S., Elith, J., Guillera-Arroita, G., Hauenstein, S., Lahoz-Monfort, J. J., Schröder, B., Thuiller, W., Warton, D. I., Wintle, B. A., Hartig, F., & Dormann, C. F. (2017). Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. *Ecography*, *40*(8), 913–929. https://doi.org/10.1111/ecog.02881

Rogora, M., Frate, L., Carranza, M. L., Freppaz, M., Stanisci, A., Bertani, I., Bottarin, R., Brambilla, A., Canullo, R., Carbognani, M., Cerrato, C., Chelli, S., Cremonese, E., Cutini, M., Di Musciano, M., Erschbamer, B., Godone, D., Iocchi, M., Isabellon, M., … Matteucci, G. (2018). Assessment of climate change effects on mountain ecosystems through a cross-site analysis in the Alps and Apennines. *Science of the Total Environment*, *624*, 1429–1442. https://doi.org/10.1016/J.SCITOTENV.2017.12.155

Ruiz-Olmo, J., Calvo, A., Palazón, S., & Arqued, V. (1998). Is the Otter a bioindicator? *Galemys*, *10*, 227–237.

Scorpio, V., Loy, A., Di Febbraro, M., Rizzo, A., & Aucelli, P. (2016). Hydromorphology meets mammal ecology: River morphological quality, recent channel adjustments and otter resilience. *River Research and Applications*, *32*(3), 267–279. https://doi.org/10.1002/rra

Sirami, C., Caplat, P., Popy, S., Clamens, A., Arlettaz, R., Jiguet, F., Brotons, L., & Martin, J. L. (2017). Impacts of global change on species distributions: Obstacles and solutions to integrate climate and land use. *Global Ecology and Biogeography*, *26*(4), 385–394. https://doi.org/10.1111/geb.12555

Swets, J. A. (1988). Measuring the accuracy of diagnostic systems. *Science*, *240*(4857), 1285–1293. https://doi.org/10.1126/science.3287615

Taheri, S., García-Callejas, D., & Araújo, M. B. (2021). Discriminating climate, land-cover and random effects on species range dynamics. *Global Change Biology*, *27*(6), 1309–1317. https://doi.org/10.1111/gcb.15483

Thompson, L. M., Staudinger, M. D., & Carter, S. L. (2015). *Summarizing Components of U.S. Department of the Interior Vulnerability Assessments to Focus Climate Adaptation Planning: U.S. Geological Survey Open-File Report 2015–1110*.

Thompson, R. M., Beardall, J., Beringer, J., Grace, M., & Sardina, P. (2013). Means and extremes: Building variability into community-level climate change experiments. *Ecology Letters*, *16*(6), 799–806. https://doi.org/10.1111/ele.12095

Thuiller, W., Lafourcade, B., Engler, R., & Araújo, M. B. (2009). BIOMOD - a platform for ensamble forecasting of species distribution. *Ecography*, *32*, 369–373. https://doi.org/10.1111/j.1600-0587.2008.05742.x

Tiago, P., Pereira, H. M., & Capinha, C. (2017). Using citizen science data to estimate climatic niches and species distributions. *Basic and Applied Ecology*, *20*, 75–85. https://doi.org/10.1016/j.baae.2017.04.001

Titeux, N., Henle, K., Mihoub, J. B., Regos, A., Geijzendorffer, I. R., Cramer, W., Verburg, P. H., & Brotons, L. (2017). Global scenarios for biodiversity need to better integrate climate and land use change. *Diversity and Distributions*, *23*(11), 1231–1234. https://doi.org/10.1111/ddi.12624

van Strien, A. J., Van Swaay, C. A. M., & Termaat, T. (2013). Opportunistic citizen science data of animal species produce reliable estimates of distribution trends if analysed with occupancy models. *Journal of Applied Ecology*, *50*(6), 1450–1458. https://doi.org/10.1111/1365-2664.12158

Warren, R., Price, J., Graham, E., Forstenhaeusler, N., & VanDerWal, J. (2018). The projected effect on insects, vertebrates, and plants of limiting global warming to 1.5°C rather than 2°C. *Science*, *360*(6390), 791–795. https://doi.org/10.1126/science.aar3646

Williams, S. E., Shoo, L. P., Isaac, J. L., Hoffmann, A. A., & Langham, G. (2008). Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biology*, *6*(12), 2621–2626. https://doi.org/10.1371/journal.pbio.0060325

Xu, J., Badola, R., Chettri, N., Chaudhary, R. P., Zomer, R., Pokhrel, B., Hussain, S. A., Pradhan, S., & Pradhan, R. (2019). Sustaining biodiversity and ecosystem services in the Hindu Kush Himalaya. In P. Wester, A. Mishra, A. Mukherji, & A. B. Shrestha (Eds.), *The Hindu Kush Himalaya Assessment* (pp. 127–165). Springer International Publishing.

Xu, J., Grumbine, R. E., Shrestha, A., Eriksson, M., Yang, X., Wang, Y., & Wilkes, A. (2009). The melting Himalayas: Cascading effects of climate change on water, biodiversity, and livelihoods. *Conservation Biology*, *23*(3), 520–530. https://doi.org/10.1111/j.1523-1739.2009.01237.x

BIOSKETCH

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