Forecasting the combined effects of climate and land-use change on Mexican bats

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Key words: Chiroptera, dispersal, ensemble species distribution models, environmental change, environmental suitability, megadiverse regions.

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(A) ABSTRACT

Aim: Climate and land-use change are among the most important threatening processes driving biodiversity loss, especially in the tropics. Although the potential impacts of each threat have been widely studied in isolation, few studies have assessed the impacts of climate and land cover change in combination. Here, we evaluate the exposure of a large mammalian clade, bats, to multiple scenarios of environmental change and dispersal to understand potential consequences for biodiversity conservation.

Location: Mexico

Methods: We used ensemble species distribution models to forecast changes in environmental suitability for 130 bat species that occur in Mexico by 2050s under four dispersal assumptions and four combined climate and land-use change scenarios. We identified regions with the strongest projected impacts for each scenario and assessed the overlap across scenarios.

Results: The combined effects of climate and land-use change will cause an average reduction of environmental suitability for 51% of the species across their range, regardless of scenario. Overall, species show a mean decrease in environmental suitability in at least 46% of their current range in all scenarios of change and dispersal. Climate scenarios had a higher impact on species environmental suitability than land-use scenarios. There was a spatial overlap of 43% across the four environmental change scenarios for the regions projected to have the strongest impacts.

Main conclusions: Combined effects of future environmental change may result in substantial declines in environmental suitability for Mexican bats even under optimistic scenarios. This study highlights the vulnerability of megadiverse regions and an indicator taxon to human disturbance. The consideration of combined threats can make an important difference in how we react to changes to conserve our biodiversity as they pose different challenges.

Key words: Chiroptera, dispersal, ensemble species distribution models, environmental change, environmental suitability, megadiverse regions.

(A) INTRODUCTION

Humans have affected most of the surface of the planet causing considerable ecosystem change (Sanderson et al., 2002), where land use and climate change are considered as the primary direct drivers of the current biodiversity crisis (Pereira et al., 2012). Forecasts of the effects of environmental change on biodiversity are useful to examine threats operating at different scales in space and time, and to locate vulnerable and important conservation areas (Coreau et al., 2009). Predictions should cover multiple threats (e.g. climate and land-use change) as it is complicated to determine how species may react to different threats and their interactions (Travis, 2003; Brook et al., 2008). However, most biodiversity scenarios consider single threats in their analysis, mostly focusing exclusively in climate change and overlooking land use change (Titeux et al., 2016).

The analysis of single threats in vulnerability assessments restricts our understanding of their negative or positive consequences, limits our ability to set effective mitigation and management plans and will affect model predictions. Climate change shifts the distribution of suitable areas, thereby forcing species to track their bioclimatic niches (Walther et al., 2002). Land-use is likely to impede species movements by converting climatic suitable habitats into human-made landscapes unsuitable for dispersal and can alter regional climates otherwise unaffected by climate change (Costa & Foley, 2000; Brook et al., 2008). Moreover, abandonment of previously disturbed areas (e.g. timber and agriculture) may offer an opportunity for habitat restoration to recover species and help them cope with current and future changes (Navarro & Pereira, 2012).

Although consideration of combined impacts of climate and land-use change is desirable, it is a difficult task. Future scenarios might not be available or those available might not have an adequate spatial, thematic or temporal resolution. Modelling land-use change is complicated because models should be constructed with many related variables involving physical and socioeconomic factors that are continuously changing. For example, land use change maps often failed to represent landscape structure or fragmentation at fine scales and do not consider changes in land management regimes. In addition, some studies do not consider the effect of land use change useful to assess future biodiversity impacts or do consider climate change to be the biggest threat (Titeux et al., 2016).

It is also important to include a range of socioeconomic and dispersal scenarios. As changes are unpredictable, the consideration of different scenarios of change can help identify and quantify uncertainties in models, and both on species vulnerability to different magnitudes of change and the areas that will be most impacted (Pompe et al., 2008; Barbet-Massin et al., 2012). Modeling dynamic environmental variables is particularly important for fine spatial resolution studies, in areas affected by different threats and when variables may interact with each other (Barbet-Massin et al., 2012; Regos et al., 2015). However, so far, most studies have assumed untransformed land-use over time (e.g., Pearson et al., 2014) or included single land-use scenarios (Hughes et al., 2012; but see Jetz et al., 2007; Pompe et al., 2008; Barbet-Massin et al., 2012). Dispersal is a central process influencing species survival when the environment is variable (Travis et al., 2013). Consideration of the movement capacity of species is essential to better understand species limitations to cope with unfavourable environmental conditions (Travis et al., 2013). However, the lack of information on the dispersal capacity for most species has limited its use in predictive models and the majority of studies modelling environmental change assume that species have either unlimited or no-dispersal (Urban, 2015).

Geographic vulnerability assessments suggest that the tropics are where the combined impact of land use and climate change is projected to have the greatest effects as these areas harbour the majority of Earth's species and the highest number of threatened species (Mittermeier et al., 1997; IUCN, 2015). Moreover, the tropics are projected to experience more novel climates (Mora et al., 2013), and higher rates of land-use change, global warming and invasive species (Sala et al., 2000; Brooks et al., 2006; Malcolm et al., 2006). Mexico embodies a substantial conservation challenge as it is one of the most biodiverse countries (Mittermeier et al., 1997), and it has been identified as particularly vulnerable to environmental change and biodiversity loss (Malcolm et al*., 2006;* Visconti et al., 2011). However, information concerning future effects of human-caused changes on Mexican biodiversity is scarce since most studies have assessed small regions (e.g. García et al., 2013), included limited numbers of species (Monterrubio-Rico et al., 2015) and analysed single threats (Peterson et al., 2002).

Here, we examine the combined impacts of climate and land-use in Mexico, with a specific focus on bat biodiversity. Bats make up to 26% of Mexico's mammalian fauna and are recognized to be important bioindicators to understand the impacts of environmental change in a broader context (Medellín et al., 2008; Jones et al., 2009). They respond in terms of richness, abundance and physiology to changes in land use, management intensities and extreme weather events (Sherwin et al., 2012). Bats have a relatively stable taxonomy thus can be identified and monitored with certainty. They pose strong mutualistic relationships with plants and rely on the stability of other animal populations (e.g. fishes and insects) which makes them highly sensitive to environmental stressors and disturbances that may disrupt those interactions (Jones et al., 2009; Jone, 2012). Few environmental change studies have evaluated Mexican mammals and those are either general (Peterson et al., 2002), or focused on non-bat species (Vidal-García & Serio-Silva, 2011). We used ensemble models to forecast changes in habitat suitability for 130 bat species that occur in Mexico under four dispersal assumptions and four combined climate and land-use socio-economic development scenarios for the 2050s. We aimed to assess the impacts of environmental change on bat species by looking at changes in environmental suitability for each scenario, and to then identify the regions with the strongest projected impacts of environmental change for each scenario and their congruence across scenarios.

(A) METHODS

We collated occurrence records across continental America for bat species that occur in Mexico from online repositories, published and unpublished sources and our collected material (a list of the data sources is found in Appendix S1 in Supporting Information). We excluded records prior to 1970 to better match the recording period of the species data with the environmental variables. We performed a data-cleaning process to improve the quality of the database as follows: 1) records not determined to species, with obvious errors in the assigned locality (i.e., outside the country boundaries, occurring at the sea or with locality and coordinates mismatches) and without coordinates or date were excluded; 2) we assumed species' identifications were correct, scientific names were standardized according to Simmons (2005) and occurrences where taxonomy could not be correctly assigned were removed; 3) duplicated records were removed if they could be determined. After this cleaning process, we had a total of 85,816 bat occurrence records from 24,476 unique localities at 5 arc minutes latitudinal-longitudinal resolution (10 km^2 at the equator).

(B) Environmental variables

Climate data: We used four bioclimatic variables at 5 arc minutes resolution (Hijmans et al., 2005) for present and future projections as follows: (i) Mean Temperature of Warmest Quarter; (ii) Mean Temperature of Coldest Quarter; and (iii) Annual Precipitation and (iv) Precipitation Seasonality. We selected these variables to reflect plausible constraints on energy, water and temperature which contribute to determine bat distributions (Sherwin et al., 2012), to adequately represent environmental variability in Mexico (Garcia, 2004) and to reduce multicollinearity (all variable with a Pearson correlation $r < 0.6$). For future climate conditions, we selected two General Circulation Models (GCMs) (CCSM4 and MIROC-ESM-CHEM) and two contrasting greenhouse gas concentration trajectories (Representative

Concentration Pathways-RCP) for 2050s: a steady decline pathway with CO_2 concentrations of 360 ppmv (RCP-2.6) and an increasing pathway with CO_2 reaching around 2000 ppmv (RCP-8.5) (IPCC, 2013).

Land-use data: Current and future land-use maps were obtained from van Eupen et al. (2014). They use dynamic models for eight land-use classes across Latin America from 2005 to 2050 at a spatial resolution of ±1 km^2. For analysis, all land-use variables were resampled to fit the resolution of the climatic variables and some of the original classes were merged to give proportions of each grid cell comprised in four classes: (i) forest; (ii) shrubland; (iii) grassland; and (iv) cropland. These land use variables represent the main vegetation types in the country (Rzedowski, 2006). We selected two land-use projections based on two extreme socio-economic contexts (SSPs): 1) a 'sustainable heaven' scenario (SSP1) assuming a reduction on resources use, dependency on fossil fuels and deforestation within protected areas; and 2) a 'business-as-usual' scenario (SSP5S) where land degradation will continue without land protection and development will be oriented towards economic growth dominated by fossil fuels (for a detailed description on the land use models see Appendix S2). We combined the two land-use and the two climate change scenarios to obtain a total of four combined environmental change projections: 1) RCP-2.6+SSP1 (optimistic combined scenario), 2) RCP-2.6+SSP5S, 3) RCP-8.5+SSP1, 4) RCP-8.5+SSP5S (pessimistic combined scenario).

(B) Species distribution models

We modelled 130 bat species (94% of the known species in Mexico) with >5 presence points that occur in Mexico and applied ensemble models to make current and future predictions using four algorithms: Multivariate Adaptive Regression Splines (MARS), Boosted Regression Trees (BRT), Generalized Additive Models (GAM) and Generalized Linear Models (GLM) (Elith et al., 2006). We calibrated BRT and MARS models to select the best parameters for model building of each species. For BRT, we fitted all combinations of a) regularization: lr = 0.05, 0.01, 0.005, 0.001; b) tree complexity = tc = 1, 3, 5, 7; and c) number of trees: nt= 500, 1000, 1500, 2000. For MARS, we fitted all combinations of a) degree = 1, 2, 3; b) penalty = 1, 2, 3; and c) threshold = 0.05, 0.01, 0.005, 0.001, 0.0005. We used the target-group approach suggested by Phillips et al. (2009) to generate pseudo-absences. Pseudo-absence data (i.e. 'back-ground' data) are usually drawn at random from the entire region, whereas presence data is often spatially biased toward easily accessed areas. Since the spatial bias generally results in environmental bias, the difference between presence data and background sampling may lead to inaccurate models. To correct the estimation, pseudo-absences were taken from the presence points of the other bat species recorded. As the bias in the presence data is the same for all species, better results can be obtained by using pseudo-absences within the presence points of the other species rather than using randomly selected pseudo-absences. We produced the pseudo-absence grid using all bats occurrence data available for continental America in GBIF. We used all grid cells that had at least one bat record (N=7,228) to create a unique baseline set of pseudo-absences for all species.

We calibrated the models using the full range of the species across continental America to capture the entire environmental gradient of the species distributions, which improves model predictions in time and space (Pearson et al., 2004). We then analysed projections only in Mexico. We calibrated the models using an 80% random sample of the data for training and the remaining 20% for testing. We repeated this procedure five times (5 fold cross-validation) and selected the best parameters based on values of the Area Under the Receiver Operating Characteristic Curve (AUC) (Fielding & Bell, 1997) for each algorithm and species to build the final models. The predictive performance for the final models was evaluated using the same procedure. We additionally tested model accuracy with Boyce´s index (Hirzel et al., 2006) using the ecospat R package (Di Cola et al., 2017) (see Table S1 for model scores on individual species).

For the future projections, we built ensemble models using the weighted mean distribution suitability scores (following Marmion et al., 2009). We included 100% of the occurrence data for projections because the removal of presence records has a negative effect on model performance, and the random removal of presence records adds a considerable amount of uncertainty in future projections (Araújo et al., 2009). For each species, we ran each possible modelling combination: 2 time periods (current and for 2050s) X 2 general circulation models (GCMs) X 2 climate scenarios (RCPs) X 2 land use scenarios (SPPs). However, different GCMs add methodological uncertainty in model predictions (Beaumont et al., 2008). One approach to incorporate this uncertainty into model projections is averaging model outcomes from different GCMs. Hence, we averaged the predictions obtained from each SDMs based on each GCM across the two GCMs, which resulted in 8 predictions per species (2 time periods X 2 SSP x 2 RCP). All models were built with the biomod2 R package (Thuiller et al., 2009) in R version 3.0.2 (R Development Core Team, 2013).

(B) Dispersal assumptions

Modelling more realistic dispersal scenarios for Mexican bats is ideal, but is impractical at the moment considering the limited information available. Research on bats' natal dispersal is almost non-existent and the existing information is on migration distances, swarming events and feeding movements, and these do not necessarily reflect species' ability to colonise newly suitable areas (Popa-Lisseanu & Voigt, 2009; Moussy et al., 2013). Reported movement distances range up to 1,905 km in long-distance migrations, 100-800 km during seasonal movements, and 10-80 km for swarming events (Fleming & Eby, 2003; Hutterer et al., 2005; Kerth & Petit, 2005; Ellison, 2008). We therefore present results using a no-dispersal scenario because most mammals are likely to fail to keep up with environmental change (Moritz et al., 2008; Schloss et al., 2012). However, in spite of the data limitation about bat natal dispersal, we tested the sensitivity of our results applying three additional partial-dispersal assumptions for the least and most extreme environmental scenarios (see Appendix S3 for details on the methods and results for the dispersal scenarios).

(B) Assessing changes in environmental suitability

We examined changes in habitat suitability rather than making inferences about distributional changes because this approach avoids uncertainties rising from converting model scores into binary simulations of presence and absence (Hof et al., 2011). We used the predicted change in environmental suitability from the models to assess the impacts of environmental change on bat species current range. The change in environmental suitability was calculated as the difference in environmental suitabilities between current and future conditions for each scenario (rounded to 1 decimal place). For the no-dispersal scenario, we restricted our suitability change estimates to grid cells where species currently occur based on potential distribution maps from the IUCN (IUCN, 2015). For the other three dispersal assumptions, we used the total dispersal distances to draw a buffer around the baseline (no-dispersal) IUCN range map for each species.

For each environmental change and dispersal scenario, we counted the number of species per grid cell that are projected to have a negative change in suitability between current and future conditions. However, any reduction in environmental suitability does not necessarily lead to species declines or extinctions. Therefore, we used three suitability change thresholds to assess the consistency of our results and to highlight those areas with a higher probability of species declines due to larger losses on environmental suitability. To do so, we counted those species projected to have any loss in environmental suitability, a loss of ≥25% and ≥50% loss from their current environmental suitability. Finally, based on the three suitability change thresholds (any loss in environmental suitability, moderate loss of ≥25% and large loss of ≥50%), we estimated, for each grid cell, the proportion of species present that were expected to have reduced environmental suitability (proportion of loser species). Summary of the variables used can be seen in Table 1.

(B) Identification of areas with the strongest projected impacts

We followed methods from Hof et al. (2011) to identify the regions with the strongest projected impacts of environmental change on bat diversity. First, we used the IUCN range maps for the modelled bats species to determine bat richness per grid cell by overlaying the maps and counting how many coincide in each cell. Then, we identified the 25% of all grid cells with the highest proportion of species that will lose average suitability across their current range for each scenario and each suitability change thresholds (high risk areas). We also identified the regions with the highest bat richness projected to be at higher risk (risk hotspots) by further selecting the top 25% of the grid cells with the highest current bat richness that overlaid with the high risk areas. We further looked at spatial uncertainties in estimating environmental change impacts from different scenarios by counting the number of scenarios that identified a particular grid cell as a high risk area or risk hotspot.

(A) RESULTS

(B) Changes in environmental suitability

The magnitude of change in environmental suitability was highly variable among species, but loser species were consistent across scenarios (Fig. 1). Depending on the scenario, 70 to 76 out of the 130 modelled species were projected to lose environmental suitability on average across their range. In all scenarios, 66 species (51% of the modelled species) showed decrease in suitability on average across their range (see Table S2 for details on each species and scenarios). The proportion of loser species per grid cell and the proportion of their ranges predicted to lose environmental suitability were consistent across scenarios when any suitability change was considered (Table 2). However, increasing the suitability change threshold decreased estimates of range loss across species and the mean proportion of loser species per grid cell across scenarios (Table 2). For example, with the moderate environmental suitability loss, 1% of the grid cells in the optimistic and 7% in the pessimistic scenario were identified as having at least half of their species losing environmental suitability, compared to cero grids with the large environmental suitability loss.

Losses on environmental suitability depended more on the environmental scenario than on dispersal assumptions (see Fig. S3.1 in Appendix S3). The greatest losses of environmental suitability per species can be seen with the pessimistic climate change scenarios (Fig. 2). When any suitability threshold is considered, even under optimistic land-use change scenarios, 18% of the bat species were projected to lose environmental suitability in ≥80% of their range and 35% showed losses in at least 50% of their range. In contrast, the projection using the pessimistic land-use and optimistic climate change scenarios predicted that only 8% of species would lose environmental suitability in ≥80% of their range (Fig. 2). Projections with the pessimistic climate change scenarios showed a higher percentage of grid cells with at least 50% of their species projected to lose environmental suitability (Fig. 2).

Climate and land-use change are likely to be a great concern for more than 66 Neotropical bat species (48% of the Mexican bat fauna) projected to lose environmental suitability by 2050s in at least 80% of their range regardless of the scenario. There were 11 species projected to lose environmental suitability in ≥80% of their range consistently across scenarios: *Corynorhinus townsendii, Eptesicus brasiliensis, Idionycteris phyllotis, Lasiurus cinereus, Myotis evotis, M. keaysi, M. melanorhinus, M. thysanodes, Tonatia saurophila, Rhogeessa aeneus* and *Vampyrum spectrum*. Increasing the suitability change threshold reduced the percentage of species projected to have high losses of environmental suitability across their range. For example, with a moderate loss, only 2% of the species were projected to lose environmental suitability in ≥80% of their range in all scenarios and none with the large loss. Yet, projections incorporating the pessimistic climate change scenarios showed a higher percentage of species with larger losses of environmental suitability across their range (Fig. 2).

(B) Areas with the strongest projected impacts

The overall pattern of the spatial variation in the proportion of species to lose environmental suitability was consistent across scenarios and suitability change thresholds (Fig. 3). The regions projected to have the highest proportion of loser species are the Yucatan Peninsula, dry forest of the Pacific slope, Sonoran-Sinaloan transition subtropical dry forest, Sonoran desert, Baja California desert, Gulf of California xeric scrub, northern part of the Veracruz moist forest and the Balsas dry forest.

There was a high overlap across the four scenarios for the regions identified as high risk areas, ranging from 43 to 31% depending on the suitability change threshold used. The same holds for the risk hot spots ranging from 43 to 35% based on the suitability change threshold used (Table 3). The high risk areas that were consistently highlighted in all scenarios and suitability thresholds are the Sonora, Baja California and parts of the Chihuahuan warmth deserts; west, south Pacific, Soconusco, Yucatan and Gulf of Mexico coastal plains and rolling hills; and the intermountain depressions (Fig. 4i,a-c). The risk hotspots that were consistently highlighted in all scenarios and suitability change thresholds were located in the south Pacific and Soconusco coastal plains and rolling hills; intermountain depression and north of the Gulf of Mexico coastal plains and rolling hills (Fig. 4ii,a-c).

(A) DISCUSSION

(B) Changes in environmental suitability

This is the first effort to evaluate the possible future consequences of two of the most important drivers of current global change – land-use and climate change – on Mexican bats under different combined socio-economic development scenarios for both threats and for various dispersal assumptions. Projections suggest substantial future declines in environmental suitability for the Mexican bat fauna even under optimistic socio-economic scenarios. Although the magnitude of impacts depends on the scenario, at least 51% of the Mexican bat species will likely lose environmental suitability across their ranges regardless of scenario. These results are consistent with other studies showing that large biodiversity declines are predicted even in optimistic situations (e.g. for plants: Pompe et al., 2008; for birds: Barbet-Massin et al., 2012; for bats: Hughes et al., 2012; for Mexican biodiversity: Peterson et al., 2002).

By comparing the results of the combined scenarios, we found that increasing the severity of climate change had a relatively higher impact on species environmental suitability than did increasing the severity of land-use change, which coincides with results from other studies (e.g. Barbet-Massin et al., 2012; Sohl, 2014). The apparently lower effect of land-use change might be a result of models only considering the magnitude of the change (i.e., percentage of land-use type) but not the landscape configuration of change. For instance, the variation represented by the climatic variables used across the entire species range for model calibration might have been larger than the moderate thematic resolution of the land-use variables used. Thus the climatic conditions of the species were more likely to be covered than the land-use one. Land-use effects do not only depend on the degree of change but also on their spatial structure, where spatially clumped habitat loss usually produces less fragmented landscapes that are less prone to extinction compared to scattered habitat loss (Travis, 2003). Another explanation might be that changes in climate are expected to be of greater magnitude and severity for Mexico than changes in land-use (see Fig. S1).

Differences in the results between changing the severity of land-use and climate change support conclusions from previous studies about the advantages of looking at combined effects of threats (Brook et al., 2003; Travis, 2003; García-Valdés et al., 2015; Regos et al., 2015). The analysis of single threats can mislead losses estimates because threats affect differently each area and species, and models calibration without important variables cause commission errors by overestimating suitable habitat (Yates et al., 2010; Sohl, 2014; Lehsten et al., 2015). This is particularly important for complex bioclimatic regions suffering intensive human disturbance like Mexico.

The implementation of different dispersal assumptions did not significantly alter projected risks within environmental scenarios and the importance of dispersal decreased as severity of climate change increased. Mexico represents a good example of the conservation challenges that megadiverse regions and biodiversity hotspots are experiencing, and our results also highlight the vulnerability of these areas to human disturbance (Schipper et al., 2008; Hof et al., 2011; Bellard et al., 2014). Bats, which are important indicators of human disturbance and ecosystems health, will have to migrate more than 100 km to be able to reach suitable environments by 2050s. Other taxa with poorer migration abilities are likely to suffer higher impacts. Although we did not look at individual species responses, some bat guilds are most likely to suffer the highest impacts due to their sensitivity to environmental disturbance such the gleaning insectivores, aerial insectivores and carnivores (García-Morales et al., 2013).

Bats may not be able to cope with impacts due to higher velocities of change happening in some regions than those estimated in the literature (Loarie et al., 2009; Schloss et al., 2012), or simply because there might not be environmentally suitable areas to colonize regardless of the dispersal capacity of the species. Reduced mobility is more likely due to fragmentation of suitable habitats and lack of landscape connectivity, especially in countries like Mexico with a complex array of natural biogeographic barriers and highly human-modified landscapes (Schloss et al., 2012; López-González et al., 2015).

Even though bats may be able to move over long distances, their distributional shifts and the successful establishment of populations in new areas rely on many factors besides environmental suitability such as degree of habitat fragmentation, behavioural barriers, biotic interactions and resources availability (Kerth & Petit, 2005; Campbell et al., 2009; Jones et al., 2009; Newson et al., 2009; Sherwin et al., 2012; Moussy et al., 2013). Bats not only will have to match environmental change velocities, they would also have to modify and match to the new conditions their preference for roost, food, hibernacula, and patterns of migration and reproduction (Sherwin et al., 2012). Therefore, even though our predictions account for required dispersal distances to keep up with environmental change, they are likely to underestimate losses. Modelling more realistic dispersal scenarios for Mexican bats would be ideal but impractical at the moment considering the limited information available.

(B) Areas with the strongest projected impacts of environmental change

The integrity of ecosystems and their function is already compromised in more than half of terrestrial systems (Newbold et al., 2016). Our future forecasts do not show a more promising picture. The high spatial overlap of the high risk areas and risk hotspots between scenarios further underlies the threat to the long-term persistence of biodiversity. Even the land-use scenario assuming no change within protected areas predicted impacts similar to the pessimistic one. The predicted high impacts of environmental change in some protected areas might have serious consequences for biodiversity since many of them harbour the highest numbers of endemic, endangered and restricted mammal species in Mexico and overlap with the areas identified here to be at higher risk (e.g., Calakmul and Montes Azules) (Ceballos, 2007).

Our results show bigger losses across the arid and semi-arid regions (e.g., shrublands, deciduous and temperate forests). Many of these risk hotspots are along the coast limited by water which increases risks if species are not able to adapt quickly to the new conditions. The high vulnerability of these ecosystems in Mexico (Peterson *et al*., 2002) and other parts of the world (Rebelo et al., 2010; Yackulic et al., 2011; Bilgin et al., 2012) has been previously identified. As future climatic projections estimate a severe humidity decrease and temperature increase (IPCC, 2013), bats inhabiting these regions and those reliant on temporally and spatially variable resource are likely to face greater environmental challenges and phenological mismatches (Newson et al., 2009; Sherwin et al., 2012). Environmental risks will be also high for most of the endemic Mexican bats as 12 out of the 15 endemic species occur in montane areas and three have restricted distributions in the arid regions of Baja California and the Mexican Plateau (López-González et al., 2015).

(B) Managing change

Our results are consistent even if we may adopt a more sustainable path in the near future. Similarities in the direction and spatial distribution of risk across scenarios suggest that, regardless of the magnitude of change, conservation actions for environmental change adaptation will be necessary to safeguard biodiversity. The little differences found between climatic scenarios suggest that climate mitigation efforts might not be enough to secure species survival. Thus, areas likely to be resilient to climate and land-use change should be secured (Bellard et al., 2014).

The two threats studied here pose different challenges for biodiversity conservation and conservation actions within Mexico, and other similar areas, and offer different opportunities. Proactive conservation can be focused in the drylands since they still retain a high percentage of their natural habitat and their biota is relatively intact. Here, large-scale conservation, such the protection of a large extension of land, might be achieved with relatively low investments. On the other hand, a fine-scale reactive conservation can be applied in the tropical regions which have lower biodiversity intactness (Brooks et al., 2006; Newbold et al., 2016). Mitigation strategies might include protection of areas identified here least likely to undergo significant environmental change, preservation of current protected land and reduction of habitat degradation within and outside priority conservation areas (Brooks et al., 2006; Mawdsley et al., 2009).

Monitoring programs will be important to allow tracking the actual effects of environmental change on biodiversity and provide managers with information to assess the effectiveness of conservation actions (Stein et al., 2013). This study offers the first approach to highlight the areas and species that need further attention. Yet, it remains unknown which species might be able to cope with environmental change by either shifting their ranges or adapting to the new conditions, especially in poorly studied taxa like bats. Determining more specific physiological tolerances, niche width and dispersal abilities of species will be particularly important for understanding their vulnerability and capacity to cope with the projected environmental change.

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(A) SUPPORTING INFORMATION

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

Appendix S1 Data sources.

Appendix S2 Land use models.

Appendix S3 Dispersal scenarios.

Table S1 Model scores and environmental suitability loss.

Table S2 Bat range projected to lose environmental suitability.

Figure S1 Spatial change of environmental variables.

(A) BIOSKETCH

Veronica Zamora-Gutierrez is an ecologist with a special interest in mammals. She is an active Mexican researcher in the areas of ecosystem services, bioacustic ecology, biodiversity monitoring and conservation.

Author contributions: V.Z.G. and K.E.J. conceived and designed the study, V.Z.G. collected the data, V.Z.G. analysed the data with contributions from all authors, and V.Z.G and K.E.J. led the writing with contributions from all authors.

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Table 1 Variables estimated to explain bat risks due to environmental change.

Category	Variable	Explanation
Overall diversity	Species range	Current distribution of bat species delimited by the IUCN range maps (IUCN, 2015).
	Species richness	Number of bat species that occur in a grid cell; corresponding to the IUCN range maps that overlay in each grid cell.
Dispersal assumptions	No-dispersal scenario	Estimates of change in environmental suitability are restricted to grids within species range. It is assumed one-step dispersal from the baseline distribution maps; corresponding to the IUCN range maps (IUCN, 2015). Total dispersal distance were derived from Loarie *et al.* (2009) global estimates of temperature change velocities, Schloss *et al.* (2012) global estimates of climate and land use change and an optimistic assumption of bat´s dispersal abilities.
	20 km dispersal scenario	
	60 km dispersal scenario	
	100 km dispersal scenario	
Risk for individual species	Environmental suitability change	Difference in species environmental suitability between current and future conditions rounded to 1 decimal place.
	Any suitability change threshold (any loss)	Species projected to have any loss, a loss of ≥25% or a loss of ≥50% in environmental suitability from their current environmental suitability.
	≥25% suitability change threshold (moderate loss)	
	≥50% suitability change threshold (large loss)	
Spatial distribution of threat	Proportion of losers species	Proportion between species richness per grid cell and number of species expected to have reduced environmental suitability between current and future conditions.
	High risk areas	The top 25% of all grid cells with the highest proportion of loser species.
	Risk hotspots	The top 25% grid cells identified as high risk areas that also have the highest species richness.
	Scenarios overlap	High risk areas and risk hotspots identified across the different scenarios of change.

Table 2 Proportions of bat species and species range projected to lose environmental suitability to differing degrees by the 2050s under four scenarios of change. The proportion of bat species to lose environmental suitability was estimated per each grid cell and then was averaged across all grid cells in Mexico (mean ± standard deviation). The proportion of range to lose environmental suitability per species was averaged across species (mean ± standard deviation). Results are compared across three environmental suitability change thresholds to define a loss in environmental suitability (any percentage loss, moderate loss ≥25% and large loss ≥50%). RCP-2.6+SSP1 represents the optimistic combined scenario for climate and land-use change, RCP-2.6+SSP5S and RCP-8.5+SSP1 are moderate 1 and 2 combined scenarios respectively; and RCP-8.5+SSP5S represents the pessimistic combined scenario for climate and land-use change.

	Scenario	**Any loss**	**Moderate loss**	**Large loss**
Proportion of species to lose environmental suitability	Optimistic	0.55 ± 0.16	0.18 ± 0.11	0.04 ± 0.05
	Moderate 1	0.55 ± 0.16	0.23 ± 0.12	0.06 ± 0.06
	Moderate 2	0.57 ± 0.17	0.27 ± 0.13	0.10 ± 0.07
	Pessimistic	0.57 ± 0.17	0.28 ± 0.13	0.11 ± 0.08
Proportion of range to lose environmental suitability	Optimistic	0.51 ± 0.23	0.20 ± 0.18	0.06 ± 0.10
	Moderate 1	0.53 ± 0.21	0.23 ± 0.19	0.08 ± 0.11
	Moderate 2	0.53 ± 0.25	0.28 ± 0.23	0.11 ± 0.17
	Pessimistic	0.55 ± 0.24	0.30 ± 0.23	0.13 ± 0.17

Table 3 Percentage of overlap across four environmental change scenarios for those grid cells in Mexico identified as high risk areas (25% of all grid cells with the highest proportion of species to lose environmental suitability by 2050s) and risk hotspots (overlap of the high risk areas with the 25% of the grid cells with the highest bat diversity). Results are compared across three environmental suitability change thresholds to define a negative loss in environmental suitability (any percentage loss, moderate loss ≥25% and large loss ≥50%).

	No. scenarios	**Any loss**	**Moderate loss**	**Large loss**
High risk areas	1	17	20	26
	2	29	25	28
	3	11	15	15
	4	43	40	31
Risk hot spots	1	17	22	24
	2	28	23	24
	3	12	14	17
	4	43	41	35

Figure 1 Magnitude and direction of change in environmental suitability between current and future predictions for 130 bat species according to (a) optimistic (RCP-2.6+SSP1) and (b) pessimistic (RCP-8.5+SSP5S) environmental change scenarios by 2050s. Environmental suitability ranges from 1-1000. Black circles represent overall mean suitability change per species across Mexico and the horizontal grey lines are their respective standard deviation. The vertical blue line denotes no change in suitability where values to the right and left of the line points to an increase and decrease in mean suitability. Species have the same order in both figures and are arranged in ascending magnitude (bottom to top) of environmental suitability loss in figure (b).

Figure 2 Percentage of 130 bat species losing environmental suitability by 2050s under future scenarios. The percentage of current range to lose suitability under each scenario was divided into four categories between 0% and 100%. Results are compared across three environmental change thresholds (any percentage loss, moderate loss ≥25% and large loss ≥50%) to define a negative loss in environmental suitability. RCP-2.6+SSP1 is the optimistic combined scenario for climate and land-use change, RCP-2.6+SSP5S and RCP-8.5+SSP1 are moderate 1 and 2 combined scenarios respectively; and RCP-8.5+SSP5S represents the pessimistic combined scenario for climate and land-use change.

Figure 3 Intensity of threat projected for 2050s under four scenarios of change and three suitability change thresholds (any percentage loss, moderate loss ≥25% and large loss ≥50%) to define a negative loss in environmental suitability. Intensity of threat from environmental change given as the percentage (%) of species projected to lose environmental suitability in a particular grid cell. Reddish colours denote areas with higher impacts and greenish colours areas with lower impacts. RCP-2.6+SSP1 is the optimistic combined scenario for climate and land-use change, RCP-2.6+SSP5S and RCP-8.5+SSP1 are moderate 1 and 2 combined scenarios respectively; and RCP-8.5+SSP5S represents the pessimistic combined scenario for climate and land-use change.

Figure 4 Spatial distribution and overlap between the regions with the strongest projected impacts of environmental change under four scenarios of change and three suitability change thresholds (any percentage loss, moderate loss ≥25% and large loss ≥50%) projected for 2050s. (i) High risk areas: 25% of all grid cells with the highest proportion of species to lose environmental suitability by 2050s. (ii) Risk hotspots: overlap of the high risk areas with the 25% of the grid cells with the highest bat diversity. Colours indicate the number of scenarios that coincide in identify an area with the strongest projected impacts.

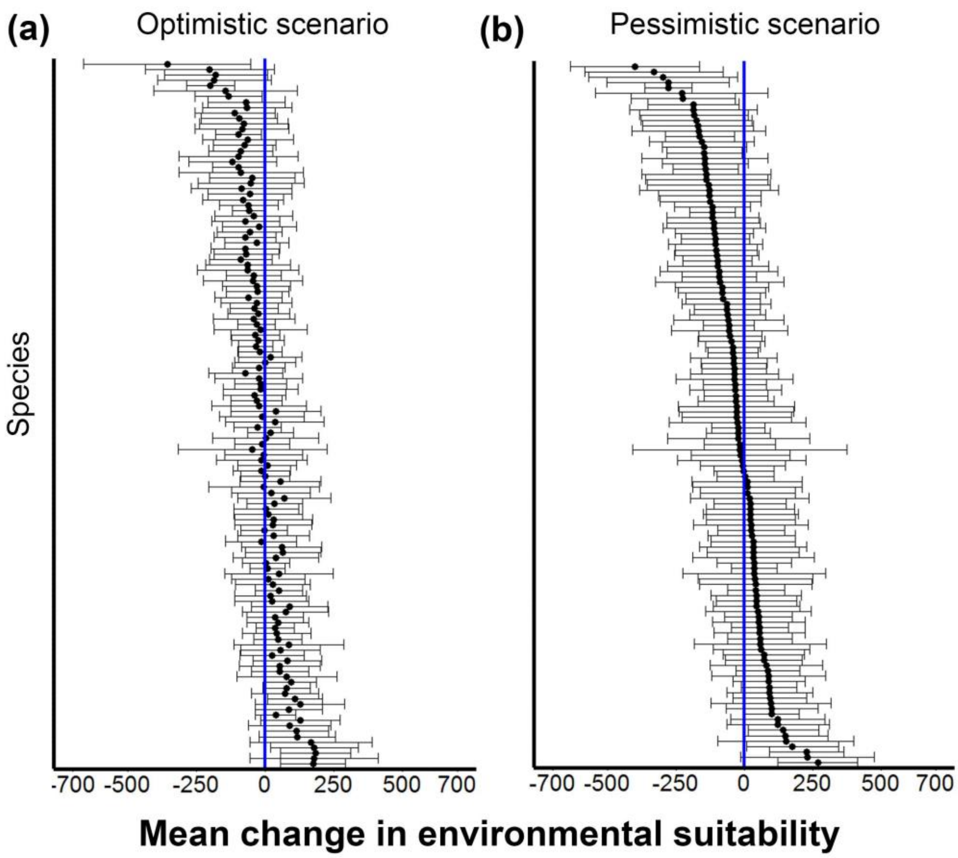
(a)
Optimistic scenario
(b)
Pessimistic scenario
Species
-700 -500 -250 0 250 500 700
-700 -500 -250 0 250 500 700
Mean change in environmental suitability

Figure 1

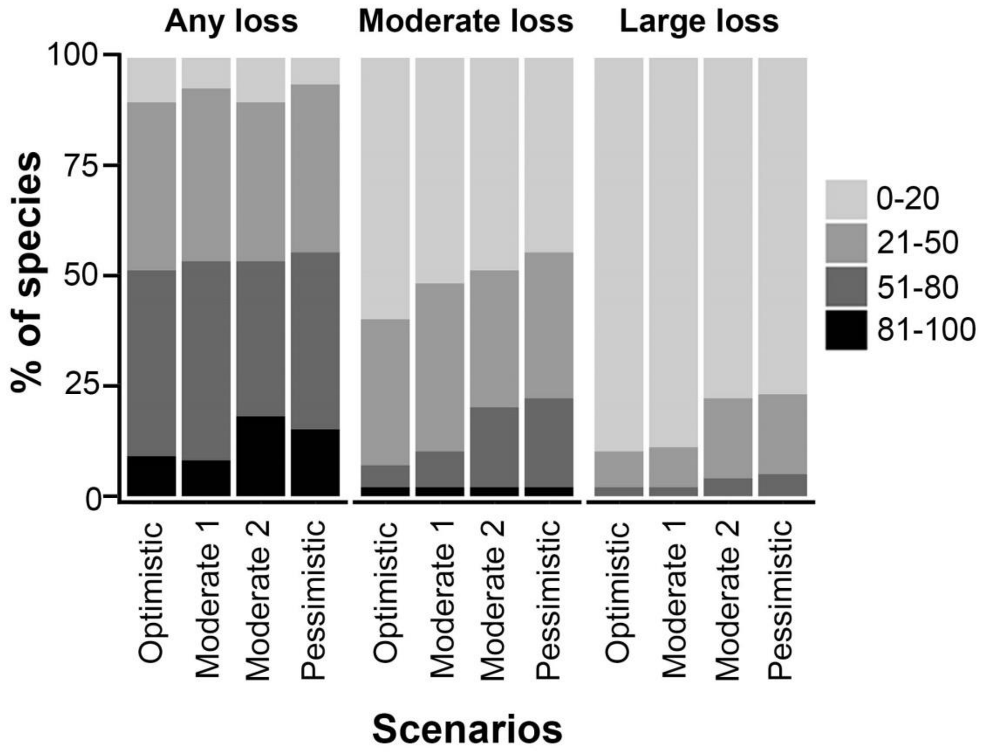
Any loss
Moderate loss
Large loss
% of species
100
75
50
25
0
0-20
21-50
51-80
81-100
Optimistic
Moderate 1
Moderate 2
Pessimistic
Scenarios

Figure 2

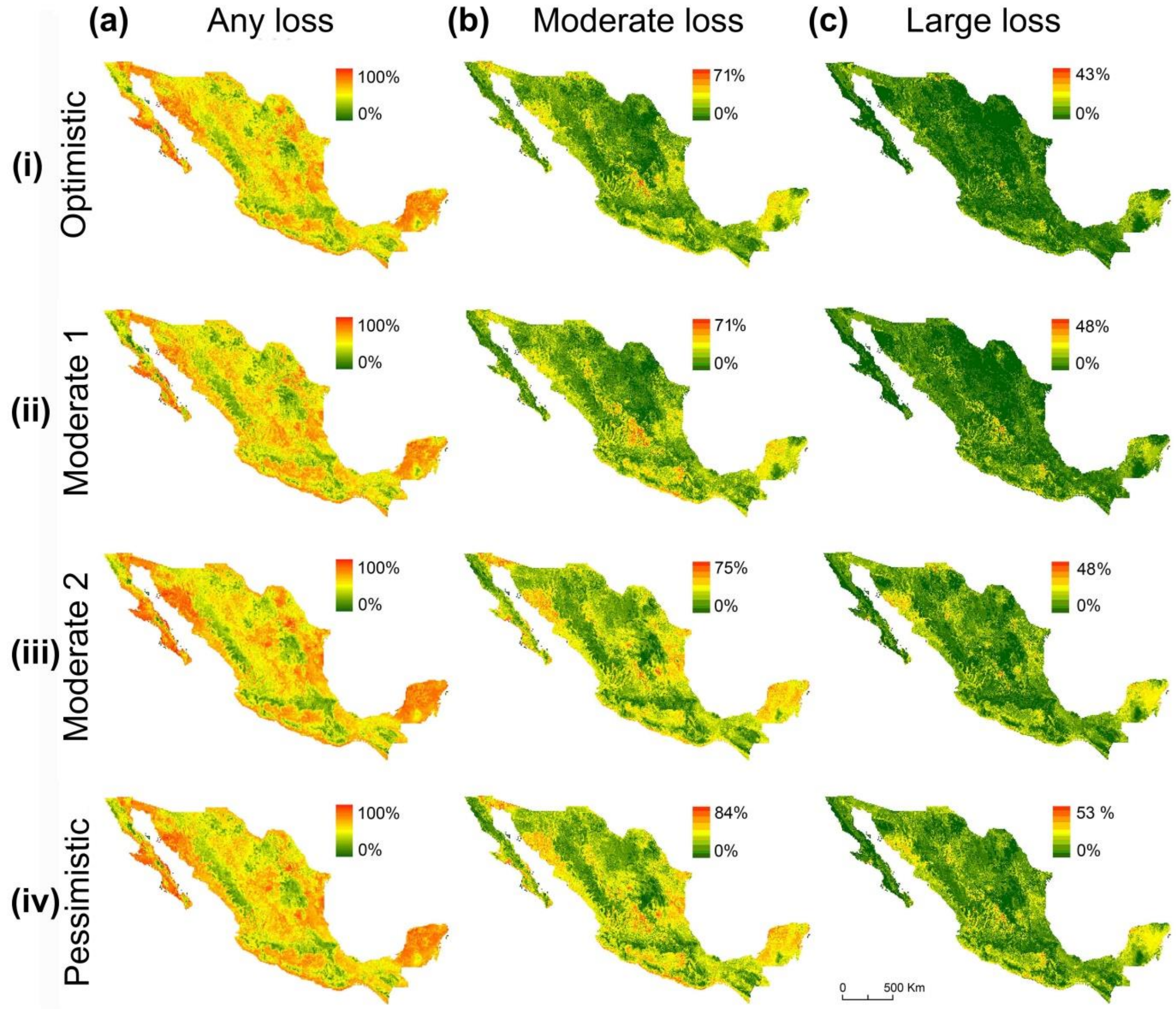
(a) Any loss
(b) Moderate loss
(c) Large loss
(i) Optimistic
(ii) Moderate 1
(iii) Moderate 2
(iv) Pessimistic
100%
0%
71%
43%
48%
75%
84%
53 %
0 500 Km

Figure 3

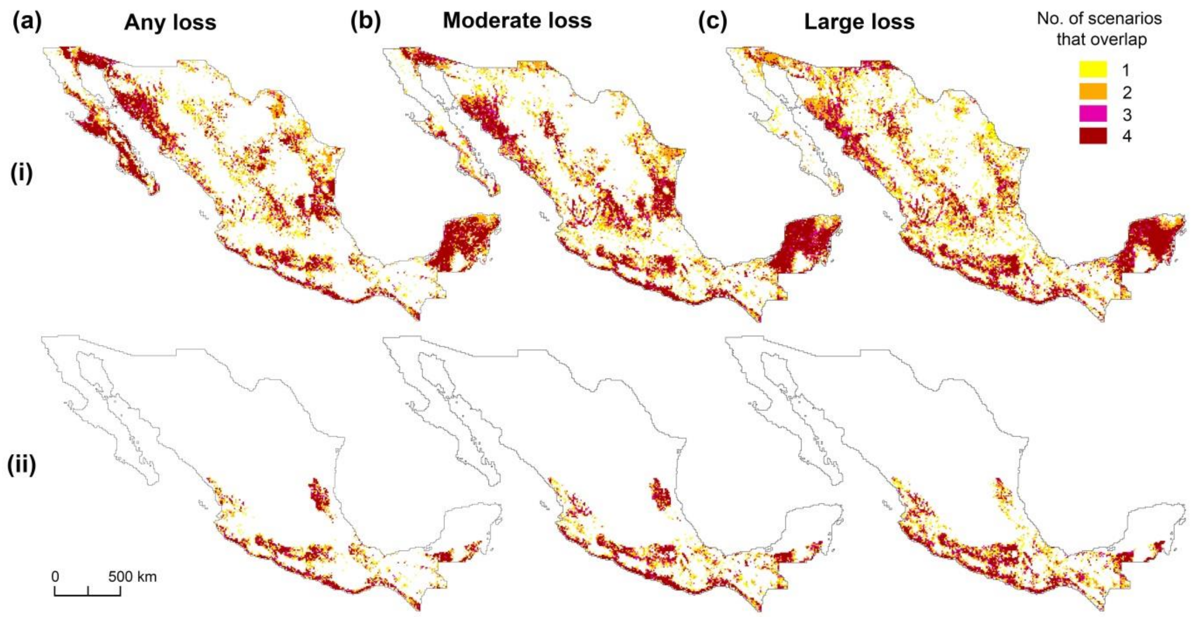
(a)
Any loss
(b)
Moderate loss
(c)
Large loss
No. of scenarios
that overlap
1
2
3
4
(i)
(ii)
0
500 km

Figure 4