



Potential individual and interactive effects of climate and land-cover changes on bats and implications for conservation planning: a case study in Vietnam

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Abstract

Climate and land-cover changes are among major threats to biodiversity. However, the interactive effects of the two threats are often overlooked in conservation planning. Using 81 bat species occurring in Vietnam as a case, we investigated the individual and interactive effects of climate and land-cover changes, highlighting the importance of this information for conservation efforts. By using species distribution models, we predicted the potential changes in range size among species and in species richness across Vietnam by the 2050s, considering projected climate and land-cover changes under two emission scenarios. Our results revealed that both threats individually would have predominantly negative effects on bats in Vietnam. Moreover, when these threats occur simultaneously, their interactions would generally intensify the impacts by mitigating individual positive effects and/or enhancing negative effects. However, we also found large interspecific and geographic variations in the direction and magnitude of these effects. Forest specialists, insectivores and cave-roosting species were predicted to be particularly vulnerable to the negative effects, with northern and southern Vietnam being more affected. These results underscore the urgent need to incorporate both climate and land-cover changes, as well as their interactions, into conservation planning for bats in Vietnam and biodiversity in general. The species-specific and spatially-explicit information regarding the impacts of the two threats can guide conservation actions, allowing us to target more manageable and less uncertain threats, as well as prioritize the protection of more vulnerable species.

Keywords Range size · Species distribution modeling · Species richness · Impact assessment · Synergistic effect · Antagonistic effect

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Introduction

Human-induced climate change and land-cover modification have long been recognized as the major threats to biodiversity (Newbold et al. 2015; Parmesan 2006). They are causing profound negative effects across biological levels (Kannan and James 2009; Krauss et al. 2010; Pardini and Nichols 2017), and thus leading to massive loss of biodiversity and degradation of associated ecosystem services (Gaston et al. 2003; Newbold et al. 2015; Parmesan 2006). In particular, changes in species distributions and diversity driven by the two environmental changes not only damage ecosystem integrity (Buisson et al. 2013; Zolkos et al. 2015), but also threaten human wellbeing (Newbold 2018; Pecl et al. 2017). As the two environmental changes are expected to continue or become even greater in the future (IPCC 2021; Reid et al. 2005), understanding and predicting the impacts are critical for conserving biodiversity under the rapidly changing environment.

Climate and land-cover changes can have non-additive effects on biodiversity, exhibiting synergistic or antagonistic interactions (Mantyka-Pringle et al. 2012; Oliver and Morecroft 2014). Synergistic interactions occur when one change enhances the impact of the other, while antagonistic interactions arise when one change mitigates the effects of the other. A synergistic effect can be observed if one change increases a species' vulnerability to, or reduces its adaptive ability toward, the other change. For instance, habitat loss can hinder the range expansion of several butterfly species in response to warming climates (Hill et al. 2001). Additionally, increased climate variability resulting from climate change can potentially amplify inter-annual fluctuations in species population size. Consequently, this increased variability may necessitate a larger amount of habitat to sustain the population, thereby rendering the population more vulnerable to habitat loss or fragmentation (Verboom et al. 2010). In contrast, if one environmental change enhances species' adaptability to the other, an antagonistic effect may occur. For instance, rising temperatures can mitigate the adverse effect of habitat fragmentation on butterfly populations by enhancing their dispersal ability and colonization frequencies (Cormont et al. 2011).

Due to the diverse types of interactive effects driven by various mechanisms, understanding how climate and land-cover changes may interactively influence biodiversity is critical for accurately assessing and predicting their impacts and for making effective conservation strategies (Brook et al. 2008; Mantyka-pringle et al. 2015; Opdam and Wascher 2004). However, investigating their interactive effects is difficult. The diverse mechanisms and scales at which the two environmental changes operate pose challenges for mechanistic or statistical integration of their effects and interactions into impact assessments (Newbold et al. 2020; Opdam and Wascher 2004; Tobias et al. 2021). Variations in biodiversity responses across taxa and geographic areas further impede the generalization of case studies and development of conservation strategies (Mantyka-pringle et al. 2012; Newbold et al. 2020; Segan et al. 2016). Therefore, most previous impact assessments investigate the two changes in isolation or examine their combined effects without explicitly considering their interactive effects, leaving large knowledge and conservation gaps (Mantyka-Pringle et al. 2015; Oliver and Morecroft 2014).

Bats (Order Chiroptera) play important roles in various ecosystems and provide key services to humans, including pest suppression, seed dispersal and pollination (Ghanem and Voigt 2012). However, bats are particularly sensitive to climate and land-cover changes (Jones and Rebelo 2013). Changing temperatures may alter the timing and duration of bats' hibernation or torpor and thus cause their phenological mismatch with food resources or increase their sensitivity to diseases (Jones and Rebelo 2013). The distribution of many bat

species is also highly dependent on the land cover in their foraging and roosting habitats (Hayes et al. 2007). Previous studies already show that climate and land-cover changes have caused (García-Morales et al. 2016; Sachanowicz et al. 2006) and will continue to cause significant impacts on the distributions of individual bat species and diversity patterns (Costa et al. 2018; Hughes et al. 2012), posing a major threat to bat species and their conservation (Frick et al. 2019; Mickleburgh et al. 2002). However, no study, to date, has explicitly evaluated the interactive effects of these changes on bats or investigated the variations in these effects across species and geographic areas.

To fill this gap, the goal of this study was to evaluate the potential effects of climate and land-cover changes on bats by explicitly considering the interactions between these changes. Using the bats in Vietnam as a case, we (1) evaluated the individual and interactive effects of future climate and land-cover changes on the potential range size across species and species richness across the country, and (2) investigated the variations in these effects across species, functional guilds and geographic areas. The species included in the analysis represent the bat fauna of the Indochinese biodiversity hotspot (Kruskop 2013), which is one of the most important regions in terms of species diversity and endemism (Tordoff et al. 2011). They constitute approximately 9% of the bats in the world and 30% in Southeast Asia, including three Endangered and five Vulnerable species according to the Red List of Endangered Species (IUCN 2023). Both the climates and land cover in Vietnam are predicted to change rapidly in the next few decades (Koyyazin et al. 2020; MoNRE 2016), posing pressing threats to these bats. Therefore, the present study provides an ideal case to showcase the essential information on the interactive effects of climate and land-cover changes for biodiversity conservation.

Materials and methods

Study area

Vietnam, situated in Southeast Asia, covers a considerable latitudinal range. The country exhibits a significant temperature gradient, with the annual mean temperature rising from 19 °C in the northern regions to 27 °C in the southern regions. Annual precipitation varies widely, ranging from under 800 mm in the coastal southeast to nearly 5000 mm in the mountainous northeast, characterized by distinct wet and dry seasons. Generally, the degree of seasonality in both temperature and precipitation diminishes from north to south (Nguyen et al. 2000). Over the last 50 years, there has been an increase of 0.6 °C in the annual mean temperature. Projections suggest that this trend will continue, with a predicted temperature increase of 1.7–2.4 °C by the end of the current century (MoNRE 2016). Furthermore, During the same 50-year period, there has been a decrease in annual precipitation of 5.8–12.5% in the northern regions and an increase of 6.9–19.8% in the southern regions. It is estimated that both regions will experience an increase in precipitation of at least 5–15% during this century (MoNRE 2016). Approximately two-thirds of Vietnam's area is comprised of forests and grasslands, predominantly found in the northern, western and southern central regions. The remaining land is occupied by farmland and built-up areas, primarily concentrated in the two delta regions (Fig. 1a). Over the past 30 years, there has been a 10% decline in forest cover, while farmland and built-up areas have witnessed an increase of 20–30% (Poortinga et al. 2019). These trends are expected to persist if significant alterations in land-use policies do not occur (Rutten et al. 2014).

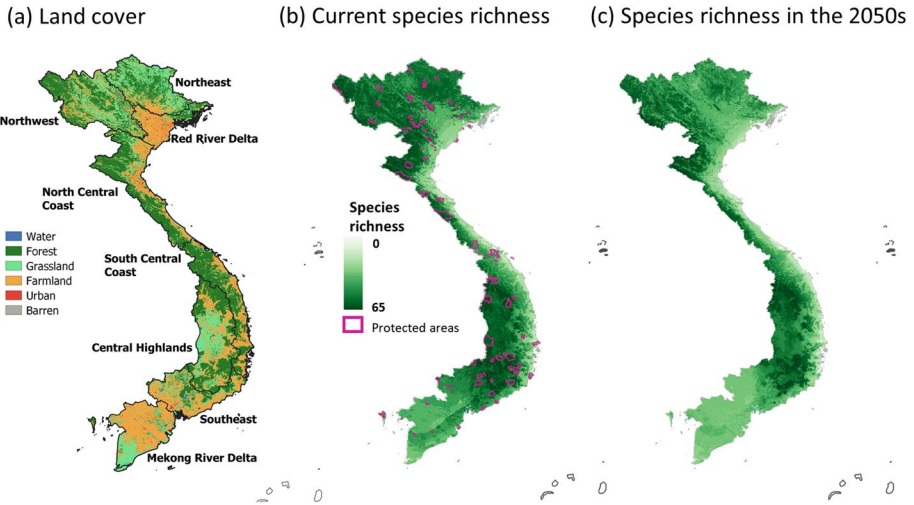


Fig. 1 Current land cover and predicted current and future species richness across Vietnam. The boundaries and the names of eight regions in Vietnam are shown in (a). The current bat species richness was derived from the predictions of the species distribution models for 81 species in Vietnam. The locations of current protected areas shown in (b) are from the World Database on Protected Areas (categories I to VI; UNEP-WCMC and IUCN 2023). The predicted species richness in the 2050s under the moderate emission scenario shown in (c) was the median of the predictions under 10 GCMs' projections

Occurrence data

We obtained the checklist of bats in Vietnam from the International Union for Conservation of Nature (IUCN 2023) and then compiled the occurrence records of the species from various sources (Table S1). First, we retrieved occurrence records of the species from the Global Biodiversity Information Facility using the *rgbif* package in R, using the accepted names of the species as searching terms (downloaded on June 3rd, 2023, DOI: <https://doi.org/10.15468/dl.28jn5y>). Only records with valid geographic coordinates and without any geographic issues were downloaded. Additionally, records associated with fossils or unknown evidence were also excluded. Second, we obtained occurrence records from 82 publications (see a list of the references in Supplementary Materials). To acquire these records, we searched for scientific names of bats, including both accepted names and synonyms, in various databases, including Web of Science, Google Scholar, and several Vietnamese journals, namely the Academia Journal of Biology (<http://vjs.ac.vn>) and the Proceedings of National Conferences on Ecology and Biological Resources (<http://iebr.ac.vn>; searched on June, 2023). Finally, we obtained additional occurrence records from the Institute of Ecology and Biological Resources in Vietnam, the Hungarian Natural History Museum, and unpublished datasets provided by the authors of this paper.

We included the occurrence records both inside and outside Vietnam to cover the full range of environmental conditions suitable for the species. To address potential temporal mismatches between occurrence data and environmental variables (climate data for the period between 1979 and 2013 and the land-cover data for 2010; see details below), we only used the occurrence records collected after 1990 in this study. We note that the data restriction may not completely resolve the mismatch issue, and the performance of our models could be affected by false species-environment associations and/or niche

truncations resulting from the mismatch (Pang et al. 2022). However, there is a potential trade-off between reducing the negative effects of the mismatch and enhancing the positive effects of incorporating additional occurrence data on model performance (Bracken et al. 2022). Given the limited availability of occurrence records for many bat species in Vietnam (Table S2), we imposed this temporal restriction on our occurrence data. In total, 8473 unique occurrence records pertaining to 116 bat species, with 81 of them having a minimum of 20 records available, were used for model building (Table S2 and Fig. S1).

We followed GBIF's taxonomy backbone as it constituted the primary source of occurrence records. However, we acknowledge that the taxonomy may not fully align with recent taxonomic revisions of Vietnamese bats (e.g. Görföl et al. 2020; Tu et al. 2018; Tu et al. 2023). This mismatch between taxonomy and recent revisions could potentially impact our modeling results for certain species. For example, if one species has been divided into multiple species, our model might capture the combined niche of these current species, leading to incorrect predictions of their responses to environmental changes if they respond differently. Resolving this taxonomic issue is challenging as taxonomy is an evolving field, and retrospectively allocated past occurrence records to currently accepted species is often infeasible. However, we believe that this issue should not undermine our overall conclusions. The taxonomic revisions affected only around 10% of the modeled species, and some species that have recently been separated from a previously recognized species still exhibit overlapping distributions (e.g. Tu et al. 2017; Tu et al. 2018), suggesting similar niches.

Environmental factors

Climate data

We obtained gridded current and future bioclimatic variables from CHELSA (Version 1.2, Karger et al. 2017). The variables for "current" climates are derived from mean monthly maximum and minimum temperatures and mean monthly precipitations spanning the period from 1979 to 2013 (Karger et al. 2017). To address the issue of multicollinearity, we conducted a correlation analysis on the 19 available bioclimatic variables. Among the variables that exhibited Spearman's correlations of higher than 0.7 with others, we selected those that held biological or ecological relevance to bat distributions. The six selected variables included the mean temperatures in the warmest and coldest quarters of the year, mean diurnal temperature range, annual precipitation, and precipitations in the warmest and coldest quarters (Fig. S2). These climate factors have been linked to aspects of bats' reproductive success, survival rates, and activity patterns (Burles et al. 2009; Furey et al. 2011; Turbill 2008).

We also obtained the future projections of the six bioclimatic variables for the period from 2041 to 2060 (hereafter referred to as the 2050s). The projections are generated by interpolating the anomalies between CMIP5 General Circulation Models (GCMs) projections and the current climates (Karger et al. 2017). To account for the uncertainties of projected future climates, we used the projections derived from 10 GCMs under two Representative Concentration Pathway (RCP) scenarios (i.e., RCP4.5 and RCP8.5). The RCP4.5 represents a moderate scenario with the CO₂ emission peaking around 2040 and then declining, while RCP8.5 represents an extreme scenario with the CO₂ emission continuing to rise in this century (IPCC 2014). The 10 GCMs used (i.e., ACCESS1-0, BCC-CSM1.1, CanESM2, CMCC-CM, CNRM-CM5, CSIRO-Mk3-6-0, GFDL-CM3, GISS-E2-R,

IPSL-CM5A-LR, and MIROC-ESM) cover a large variation in model algorithms, initial conditions, and projected outputs (Knutti et al. 2013).

Land-cover data

We obtained the current and future land-cover data from the Geographic Simulation and Optimization System (GeoSOS; <http://www.geosimulation.cn/GlobalLUCCProduct.html>). The current land-cover data is originally derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) Land Cover Type product (MCD12Q1) for the year of 2010 at 1 km spatial resolution and contains six land-cover types (Fig. 1; Li et al. 2017). Projected land-cover for the year of 2050 under the Intergovernmental Panel on Climate Change (IPCC) Special Report Emission Scenarios (SRES) scenarios B1 and A2 are simulated by using the IMAGE model with the current MODIS land cover as the initial state (Li et al. 2017). The SRES B1 and A2 scenarios used in the IPCC Fourth Assessment Report are comparable to the RCP4.5 and RCP8.5 scenarios used in the fifth report, respectively (Box 2.2 in IPCC 2014). Given that two land-cover types, namely water and barren, occupied a small portion of the study area (Fig. 1a), we extracted presence/absence information for the remaining four types (i.e., forest, grassland, farmland and urban) from the categorical land-cover data layers. This information was then used for building our species distribution models (see below).

Karst data

As karst areas provide roosts for cave bat species and sustain high bat diversity in Vietnam (Furey et al. 2010), we also included the distribution of karst as a variable to predict bat species distributions. A global data layer with polygons delimiting the areas with carbonate rocks was obtained from the World Map of Carbonate Rock Outcrops V3.0 (<https://digital.lib.usf.edu/SFS0055342/00001>). Most carbonate rocks are susceptible to karstification and thus the areas with carbonate rocks could be considered to be karst (Williams Ford 2016). However, we note that some areas with carbonate rocks may not provide suitable caves for bats, introducing an uncertainty of this data layer. We converted the data into 1-by-1-km grids by rasterizing it with the World Cylindrical Equal Area projection. In the resulting grids, the cell values represented the presence or absence of karst. We assumed that the distribution of karst areas suitable for bats does not change significantly in the next few decades, and thus used the same data layer for predicting both current and future species distributions (see below).

Species distribution modeling

We built species distribution models to predict the current and future distributions of individual bat species using Maxent (ver. 3.4.1; Phillips et al. 2006; Phillips et al. 2017) and the *dismo* package (version 1.1.4; Hijmans et al. 2017) in R (version 4.2.2). We used Maxent because it does not require absence data and has better and more consistent performance than many other algorithms (Elith et al. 2011), especially with a small number of presence locations (Hernandez et al. 2006; Wisz et al. 2008). The model for a species was built with all presence locations of the species and the current climate, land-cover and karst data mentioned above. The climate and land-cover data layers were re-projected into the same projection and resolution with the karst data. If two or more presence locations were

located within the same grid cell, we only kept one. We built our models at 1-km resolution, which is relevant to bats' habitat selection because many bat species have a home range around 1 km² (Davidson-Watts and Jones 2006; Monadjem et al. 2009). The same spatial resolution was also used in several other studies on bats (e.g., Gottwald et al. 2017; Hughes et al. 2012; Herkt et al. 2016).

We only built models for the 81 species that had at least 20 occurrence records, because this threshold limit is considered large enough for a variety of taxa in many geographic areas (Hernandez et al. 2006; van Proosdij et al. 2016; Wisz et al. 2008). Because the sampling bias of the occurrence data can reduce model performance and make a model capture sampling effort rather than the true distributions of target species (Barber et al. 2022; VanDerWal et al. 2009), we used the target-group background to correct for the bias (Phillips et al. 2009). The approach has been shown to be the most effective bias-correction approach for Maxent models (Barber et al. 2022). We used the presence locations of all 116 species, including those having less than 20 occurrence records, as the background. Because bat surveys usually target all or most bat species at a location, our occurrence records can reasonably represent the sampling effort for the whole species group, satisfying the assumption of the approach. In addition, a Multivariate Environmental Similarity Surfaces (MESS) analysis (Elith et al. 2010) showed that the target-group background data can well capture the current environmental conditions (Fig. S3a), with no extrapolation needed across Vietnam. Extrapolation occurred only for some regions in southern Vietnam under the extreme emission scenario (Fig. S3c). Therefore, we believe that the target-group background approach is appropriate in our case.

To identify the optimal model settings, we evaluated the performance of the models by testing various combinations of feature types and regularization multiplier values. Given the importance of model transferability in our study, we exploited spatial block cross-validation to evaluate model performance (Roberts et al. 2017). We divided the extent of all occurrence records into 1319 50-by-50-km blocks because it is commonly recognized that two occurrence records separated by a distance of 50 km can be considered spatially independent for bats (Betts et al. 2022; Delgado-Jaramillo et al. 2020; Hopkins et al. 2022). The blocks were then randomly allocated to 5 folds and the random allocation was repeated 100 times for each species. The allocation that achieved the most balanced distribution of species' presence and background points across the 5 folds was used for the cross-validation. We calculated the area under the receiver operating characteristic curve (AUC) as the measure of model performance. The model setting achieving the highest AUC value across the species, i.e., a regularization multiplier value of 1.5 and a combination of linear, quadratic and hinge feature types (Fig. S4), was used for building the final models. We implemented the spatial block cross-validation using the *blockCV* package (Valavi et al. 2019) and tested different model settings using the *ENMeval* package (Muscarella 2014) in R.

Current and future predictions of species potential ranges and species richness

For each species, we used its model with current environmental data layers to predict the occurrence probability in each 1 km² grid cell across mainland Vietnam. We considered a species present in a grid cell if the predicted probability was higher than a threshold value. We determined the threshold value for each species as the 10th percentile of training presences (Cao et al. 2013). We then defined the potential distribution range of a species in Vietnam as all the predicted presence grid cells of that species. For each grid cell,

we counted the species which were predicted to be present as a measure of bat species richness.

For each species, we also used its distribution model to predict its potential distributions in the 2050s with the future climate and/or land-cover data layers. We then predicted the future potential range for each species and future species richness for each grid cell using the same approach mentioned above. To examine the individual and interactive effects of climate and land-cover changes (see below), we generated the future predictions of species potential ranges and species richness under three environmental change scenarios: climate change only, land-cover change only and both changes. For the predictions under climate change only (or land-cover change only), we used future climate (or land-cover) data layers and current land-cover (or climate) and karst layers in the models. For the predictions under both changes, we used future climate and land-cover data layers and the current karst layer. We generated the predictions using the future data layers under the two emission scenarios separately. For the predictions under climate change only and both changes, we also used the future climate layers derived from each of the 10 GCMs under each emission scenario separately. Therefore, for each species, we totally generated two predictions of future potential ranges (2 emission scenarios) by the 2050s under land-cover change only, 20 predictions (10 GCMs \times 2 emission scenarios) under climate change only, and 20 predictions under both changes. We also generated 2, 20 and 20 predictions of future species richness for the 2050s for each grid cell across Vietnam under the three environmental change scenarios, respectively.

Individual, combined and interactive effects of climate and land-cover changes

We quantified the effects of climate and land-cover changes by calculating the percent change in species range size between the current and future predictions for each species and calculating the percent change in species richness for each grid cell. For the individual effects of climate and land-cover changes, we compared the current state to the future predictions under climate change only and under land-cover change only, respectively. For the combined effects, we compared the current state to the future predictions under both changes. Under each emission scenario, we evaluated the climate change-only and combined effects for different GCMs separately and calculated the medians among them.

We classified the interactive effects of climate and land-cover changes using a directional interaction classification system (Piggott et al. 2015), which is based on an additive effect model and allows the interaction types to be defined consistently no matter whether the two individual effects have the same or opposite directions. By comparing the predicted range size or species richness under both changes with the predicted values under no change (i.e., current prediction), climate change only and land-cover change only, as well as the expected value under both changes without interactions (i.e., prediction from an additive null model), we classified the interactive effects into five types (Fig. 2c, e). If the predicted value under both changes was equal to the expected value, there was no interaction and we classified the effect as additive (AD). If the predicted value was higher than expected, there was an interaction causing a positive effect. If the predicted value under both changes was also larger than any of the other predictions, the interaction was classified as positive synergistic (+S), suggesting that the interaction caused the positive effect by enhancing positive individual effects. Otherwise, the interaction was classified as negative antagonistic (−A), suggesting that the interaction caused the positive effect by mitigating negative individual effects. In contrast, if the predicted value under both changes was

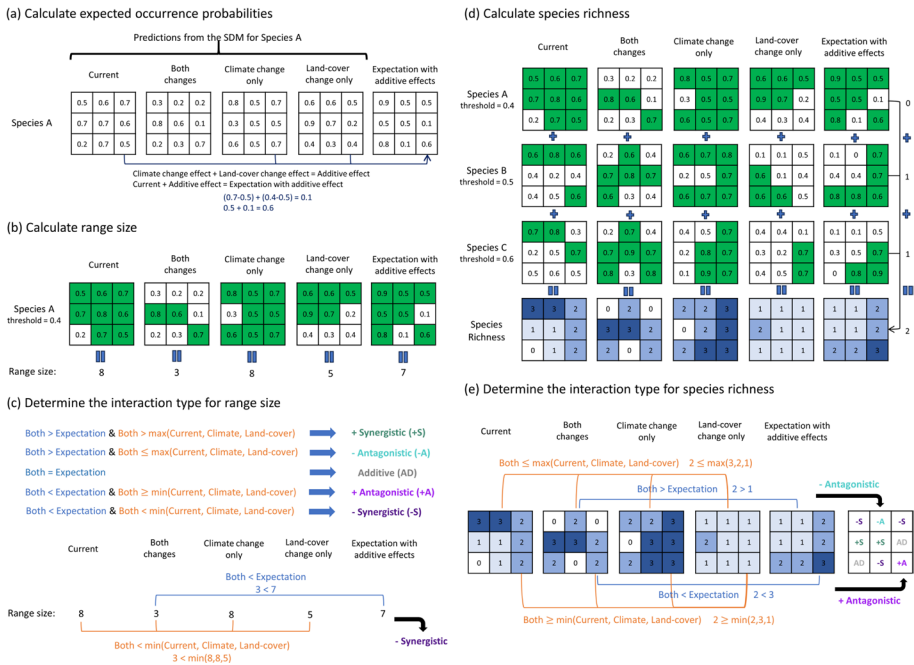


Fig. 2 Diagram demonstrating the approaches used in the study for obtaining the expected range size and species richness under both climate and land-cover changes without interactions, and for classifying interaction types. Using three hypothetical species (Species A–C) occurring in a study area containing nine grid cells, the diagram shows **a** how the expected occurrence probability is calculated for each grid cell from the model predictions under different combinations of environmental change effects; **b** how the predicted and expected range sizes are obtained from the occurrence probabilities under different combinations of environmental change effects; **c** how the type of interactions between climate and land-cover changes affecting species’ range size is determined based on the predicted and expected range sizes; **d** how expected species richness is obtained for each grid cell based on the occurrence probabilities of the three species under different combinations of environmental change effects; and **e** how the type of interactions affecting species richness is determined for each grid cell based on the predicted and expected species richness under different combinations of environmental change effects

lower than expected, there was an interaction causing a negative effect. If the predicted value was also smaller than any of the other predictions, the interaction was classified as negative synergistic (–S), suggesting that the interaction caused the negative effect by enhancing negative individual effects. Otherwise, the interaction was classified as positive antagonistic (+A), suggesting that the interaction caused the negative effect by mitigating positive individual effects. The classification of interactions was done for each GCM and emission scenario separately.

To obtain the expected range size and species richness under an additive null model, we first calculated, for a species, the predicted cell-wise changes in the occurrence probability under climate change only and land-cover change only scenarios (Fig. 2a). A cell-wise sum of the probability changes (i.e., additive changes) was added to the current probability to obtain the expected value under both changes without interactions (i.e., under an additive null model). We then converted the expected value into presence or absence of the species for each cell using the species-specific threshold, and calculated the expected range size for the species by counting the presence cells across the study area (Fig. 2b). We note that

Fig. 3 Individual and interactive effects of climate and land-cover changes on the range size of bat species in Vietnam under the moderate emission scenario. The bars in **a–c** show the predicted loss and gain of range size by the 2050s for the species under both changes (**a**), climate change only (**b**) and land-cover change only (**c**). The brown bars drawn from the current range size toward left indicate the predicted loss of range size, while the blue bars toward right indicate the predicted gain of range size. The species are ordered by their current range size within Vietnam. The species names are shown in different colors on the right to indicate different types of interactions between the two environmental changes affecting species' range size. The majority type among the predictions under 10 GCMs' projections is shown. The bar charts in **d–f** show the percentage of species in each of four levels of predicted changes in range size. The bars in **d** and **e** indicate medians of the predictions under 10 GCMs' projections, and the error bars indicate the minimum and maximum values. The bar chart in **g** shows the percentage of species whose range size was affected by different types of interactions between climate and land-cover changes. The bars indicate medians of the predictions under 10 GCMs' projections, and the error bars indicate the minimum and maximum values. The interaction types are negative synergistic (–S), positive antagonistic (+A), additive (AD), negative antagonistic (–A), and positive synergistic (+S)

this approach may result in an expected probability larger than 1 or smaller than 0, which is unreasonable, but the conversion to presence/absence data solved this issue. Finally, based on the presence/absence data across all species, we calculated the expected species richness for each cell (Fig. 2d).

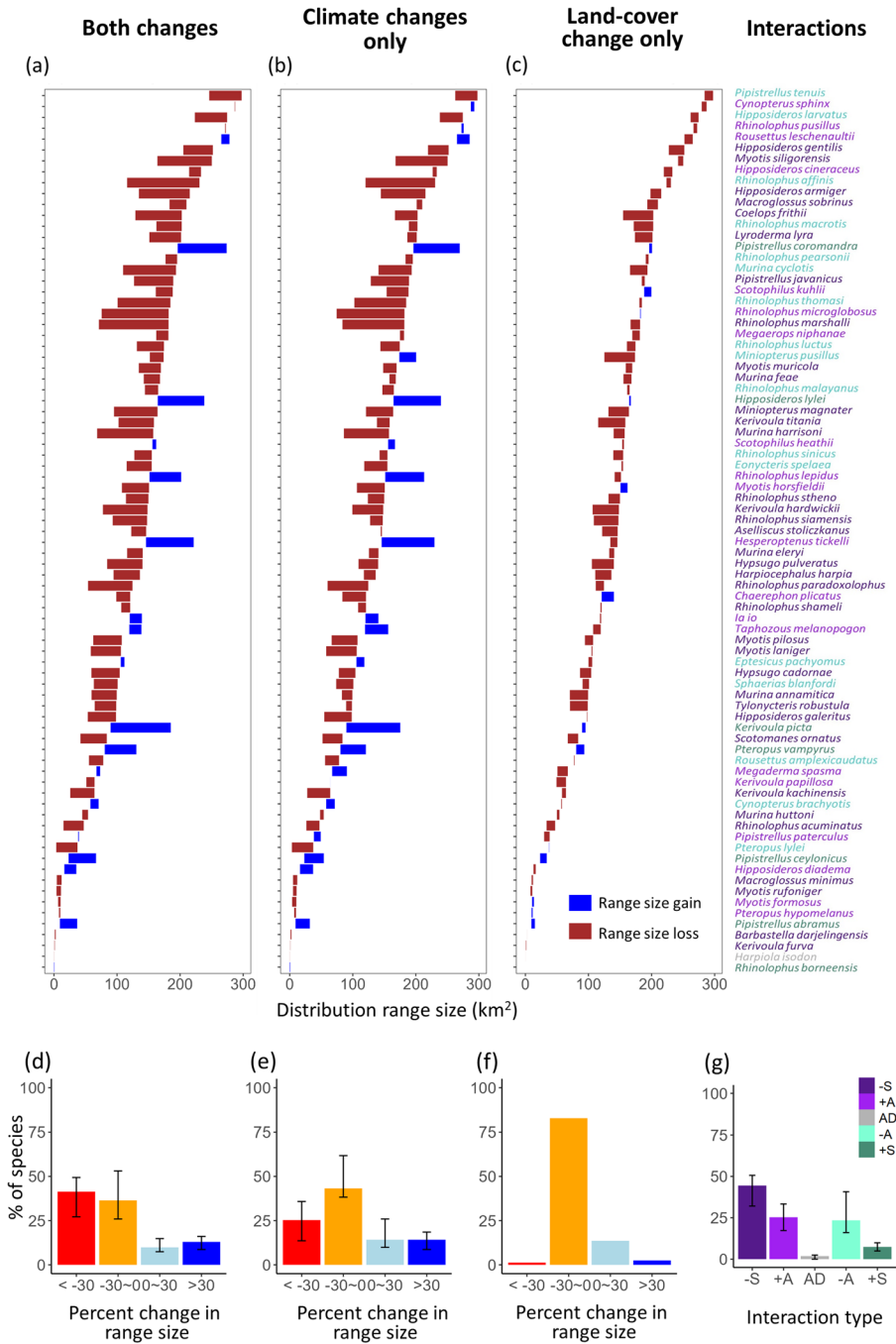
Variations among functional guilds

We compared the predicted effects of the two environmental changes and their interactions on the distributional range size of individual species and on the species richness across Vietnam between two habitat, two dietary and two roosting-site guilds. We obtained the information on the major habitat types for the species from the IUCN (2023). Based on the first level of IUCN's habitat classification scheme, all of the 81 species studied use forests as their major habitat. Twenty-seven of them use only forests (or only forests and caves) and were classified as forest specialists. All the remaining 54 species also use artificial habitats, while some can use grasslands or shrublands as well. Therefore, we classified the 54 species as habitat generalists. We classified the species into different roosting-site guilds also based on the habitat information from IUCN (2023). The species whose major habitat types include caves were classified as cave-roosting species, and the others as non-cave-roosting species. For dietary guilds, we classified the species into insectivores and frugivores based on their diets reported in the Handbook of the Mammals of the World (Wilson et al. 2019).

Results

Current potential range size and the spatial pattern of species richness

The mean AUC value of the distribution models was 0.77 ± 0.101 (mean \pm SD), with a value greater than 0.7 for 62 (76%) of the 81 bat species modeled, indicating that most models performed well. Due to the similarity in general patterns observed between including and excluding predictions from models with an AUC lower than 0.7, for both range size and species richness changes, we present the results below with all 81 species included. The results excluding the lower-AUC species are provided in the Supplementary Materials (Figs. S5–S7). Although the contributions of predictor variables in the model varied



among species, the mean temperature of the coldest quarter was generally the most important determinant of bat species distributions, followed by the mean diurnal temperature range, the precipitation of the coldest quarter and the forest cover (Fig. S8). The current

distributional ranges of the 81 species were estimated to exhibit significant variation in size, ranging from 4 to 297,545 km² within Vietnam (Fig. 3). We note that species with small distributional range size within Vietnam are not range-restricted species, but rather those with ranges primarily located outside Vietnam. The results also showed that bat richness was high in the forests and grasslands in northern Vietnam and the Central Highlands, while low in the farmlands and urban areas in the Red River and Mekong River deltas and along the eastern coast (Fig. 1a, b).

Individual and combined effects of climate and land cover changes

Our models revealed profound negative effects of future climate and land-cover changes on the potential range size of the bat species in Vietnam, with significant interspecific variation (Figs. 3 and S9). Around two-thirds of the bat species in Vietnam were predicted to lose parts or all of their potential range by the 2050s resulting from projected climate change alone under both moderate (Fig. 3b, e) and extreme emission scenarios (Fig. S9b, e). Land-cover change alone would also cause a range contraction in more than 80% of the species (i.e. 81% and 84% under the two scenarios, respectively; Figs. 3c, f, S9c, f). Although more species would suffer from land-cover change than from climate change, climate change would generally cause stronger negative effects. About 26% and 30% of the species were predicted to face a > 30% change in their range size due to climate change under the two scenarios, respectively (Figs. 3e and S9e), but only 1% and 10% of the species due to land-cover change (Figs. 3f and S9f). When both environmental changes occurred, our models showed even more negative effects. More than three-fourths (76%) of the species would have a range contraction in Vietnam by the 2050s, with 41% and 45% of the species losing > 30% of their potential range under the two scenarios, respectively (Figs. 3a, d, S9a, d).

The predicted changes in the species' potential ranges could also lead to significant changes in the bat species richness pattern in Vietnam (Figs. 4 and S10). Under the two emission scenarios, climate change alone was predicted to cause richness loss in 65% and 66% of the country and gain in 26% and 28%, respectively by the 2050s (Figs. 4f and S10f). In contrast, land-cover change would result predominantly in the loss of species richness, which occurred for 33% of land area. (Figs. 4g and S10g). When both changes occurred simultaneously, our models predicted an even larger decrease in species richness. Around 72% and 74% of the country would lose species richness by the 2050s under the two scenarios, respectively (Figs. 4e and S10e), and 25% and 33% of the land would experience a loss of more than 30%. Most areas in northern and southern Vietnam were predicted to have the highest percent loss in richness, while some areas in Central Highlands and along the eastern coast may gain richness (Figs. 4a and S10a).

Interactive effects of climate and land-cover changes

Our results showed that the interactions between future climate and land-cover changes would exacerbate the impacts on both potential range size of individual bat species and the species richness pattern across Vietnam. Under both changes, the models predicted that the interactions would negatively affect the potential range size of about two-thirds of the bat species by either enhancing the negative effect (−S in Figs. 3g and S9g) or mitigating the positive effect (+A in Figs. 3g and S9g) of individual environmental changes. Only about one-third of the species would benefit from the interactions due to either mitigated

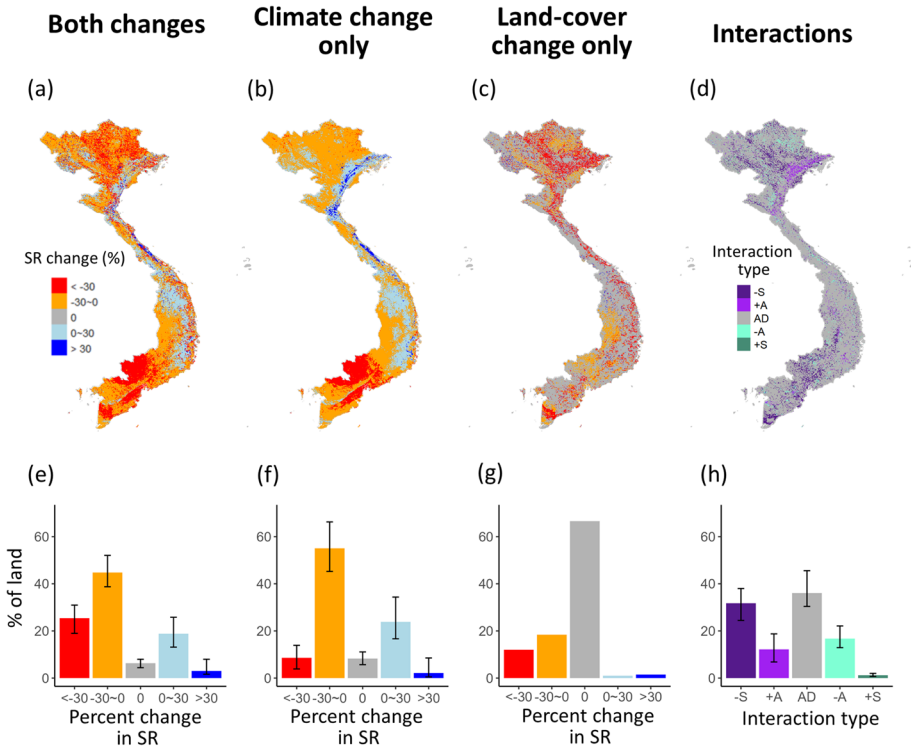


Fig. 4 Individual and interactive effects of climate and land-cover changes on species richness of bats in Vietnam under the moderate emission scenario. The maps in **a–c** show the predicted changes in species richness by the 2050s in five categories under both changes (**a**), climate change only (**b**) and land-cover change only (**c**). The change category for each 1 km² grid cell was determined by the median of the predictions under 10 GCMs’ projections. The bar charts in **e–g** show the percentage of land area in Vietnam in each of the change categories under different combinations of environmental changes. The bars in **e** and **f** indicate medians of the predictions under 10 GCMs’ projections, and the error bars indicate the minimum and maximum values. The map in **d** shows the majority type of interactions between climate and land-cover changes affecting species richness among the predictions under 10 GCMs’ projections. The bar chart in **h** shows the percentage of the land area with both climate and land-cover changes where the species richness was affected by different types of interactions. The bars indicate medians of the predictions under 10 GCMs’ projections, and the error bars indicate the minimum and maximum values. See the legend of Fig. 3 for the symbols of interaction types

negative effects (–A) or enhanced positive effects (+S). The effects of the two environmental changes on species richness were predicted to exhibit synergistic, antagonistic, or additive interactions within areas of approximately equal size (Figs. 4h and S10h). However, the interactions would be more likely to cause species richness loss by enhancing negative effects (–S) or mitigating positive effects (+A) of individual environmental changes rather than to cause richness gain by enhancing positive (+S) or mitigating negative individual effects (–A in Figs. 4h and S10h). In particular, the negative effect of climate and land-cover changes in many areas in northern and southern Vietnam would be enhanced and the positive effect of climate change in the Red River Delta would be mitigated (Figs. 4b–d and S10b–d). The predominant negative outcomes of the interactions on both potential range size and species richness pattern highlights the importance of considering the interactive effects of the two environmental changes to fully understand their impacts.

Fig. 5 Individual and interactive effects of climate and land-cover changes on the range size of bat species in different functional guilds under the moderate emission scenario. The bar charts in different rows are for different guilds, including forest specialists (a–d), habitat generalists (e–h), insectivorous bats (i–l), frugivorous bats (m–p), cave-roosting bats (q–t), and non-cave-roosting bats (u–x). The bar charts in the first three columns show the percentage of the species in different levels of predicted changes in range size under both changes, climate change only and land-cover change only, respectively. For the predictions under both changes and climate change only, the bars indicate the medians of the predictions under 10 GCMs' projections, and the error bars indicate the minimum and maximum values. The bar charts in the fourth column show the percentage of species whose range size was affected by different types of interactions. The bars indicate medians of the predictions under 10 GCMs' projections, and the error bars indicate the minimum and maximum values. See the legend of Fig. 3 for the symbols of interaction types

Variations among functional guilds of bats

The comparisons of the changes in potential range size and species richness among functional guilds of bats showed that future climate and land-cover changes and their interactions would have different effects among the guilds. Under both environmental changes, more than 88% and 92% of forest specialists and about 71% and 70% of habitat generalists would experience a range contraction under the two emission scenarios, respectively (Figs. 5a, e and S11a, e). The difference was due to stronger negative effects of both environmental changes on forest specialists, which would be further enhanced by the interactions (Figs. 5a–h and S11a–h). Larger areas in Vietnam would face richness loss in forest specialists than in habitat generalists (Figs. 6a, e, and S12a, e), mainly because of stronger negative effects of climate change on forest specialists (Figs. 6b, f and S12b, f).

Comparisons between the dietary guilds showed that climate change would cause stronger negative effects on the potential range size of insectivores than on that of frugivores (Figs. 5j, n and S11j, n). In addition, the negative effects on insectivores would be mainly enhanced by the interactions of the two environmental changes (more species in –S than in –A; Figs. 5l and S11l), while those on frugivores would be mostly mitigated (fewer species in –S than in –A; Figs. 5p and S11p). The two environmental changes would also cause substantially stronger negative effects on the richness of insectivores than on that of frugivores. Almost the entire Vietnam would face richness loss in insectivorous bats, while about 24% and 26% of the land area would have more frugivorous bats by the 2050s under the two emission scenarios, respectively (Figs. 6i, m, S12i, m). The difference resulted from more negative effects of the individual environmental changes, especially climate change, as well as more negative interactions on insectivores (Figs. 6i–p and S12i–p).

The effect of the two environmental changes on the potential range size would be similar between cave-roosting and non-cave-roosting bats (Figs. 5q–u and S11q–u). However, the effect on species richness would be more negative for cave-roosting bats. More than 74% and 75% of the land area would face richness loss in cave-roosting species, while only 54% and 58% would have fewer non-cave-roosting species by the 2050s under the two emission scenarios, respectively (Figs. 6q, u and S12q, u). The difference resulted from more negative effects of climate change and its more negative interactions with land-cover change on cave-roosting bats (Figs. 6q–x and S12q–x).

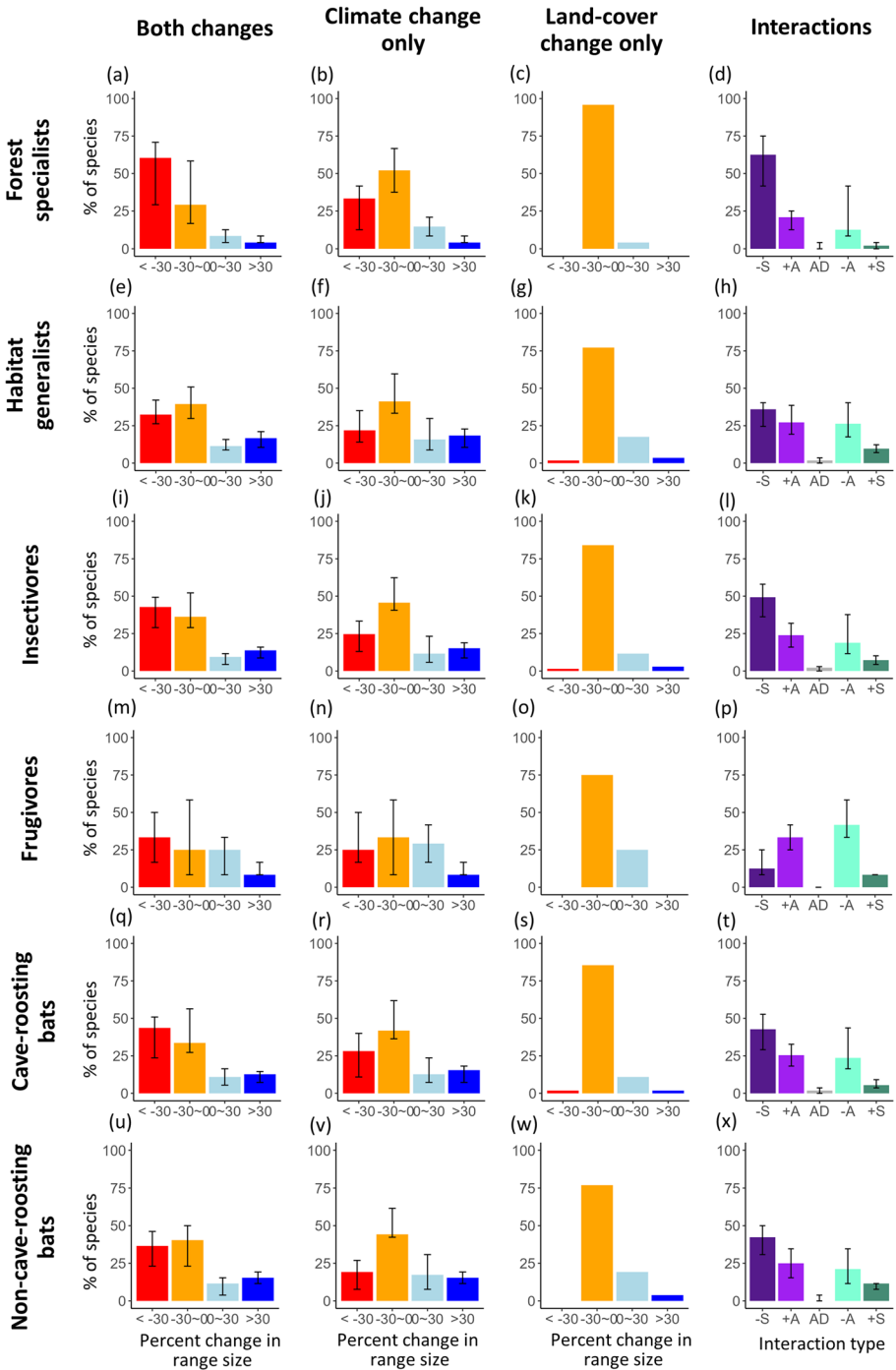


Fig. 6 Individual and interactive effects of climate and land-cover changes on the species richness in different functional guilds under the moderate emission scenario. The bar charts in different rows are shown for different guilds, including forest specialists (a–d), habitat generalists (e–h), insectivorous bats (i–l), frugivorous bats (m–p), cave-roosting bats (q–t), and non-cave-roosting bats (u–x). The bar charts in the first three columns show the percentage of the land area in Vietnam predicted to experience each of five levels of changes in species richness under both climate and land-cover changes, climate change only and land-cover change only, respectively. For the predictions under both changes and climate change only, the bars indicate medians of the predictions under 10 GCMs' projections, and the error bars indicate the minimum and maximum values. The bar charts in the fourth column show the percentage of the land area with both climate and land-cover changes where species richness was affected by different types of interactions. The bars indicate medians of the predictions under 10 GCMs' projections, and the error bars indicate the minimum and maximum values. See the legend of Fig. 3 for the symbols of interaction types

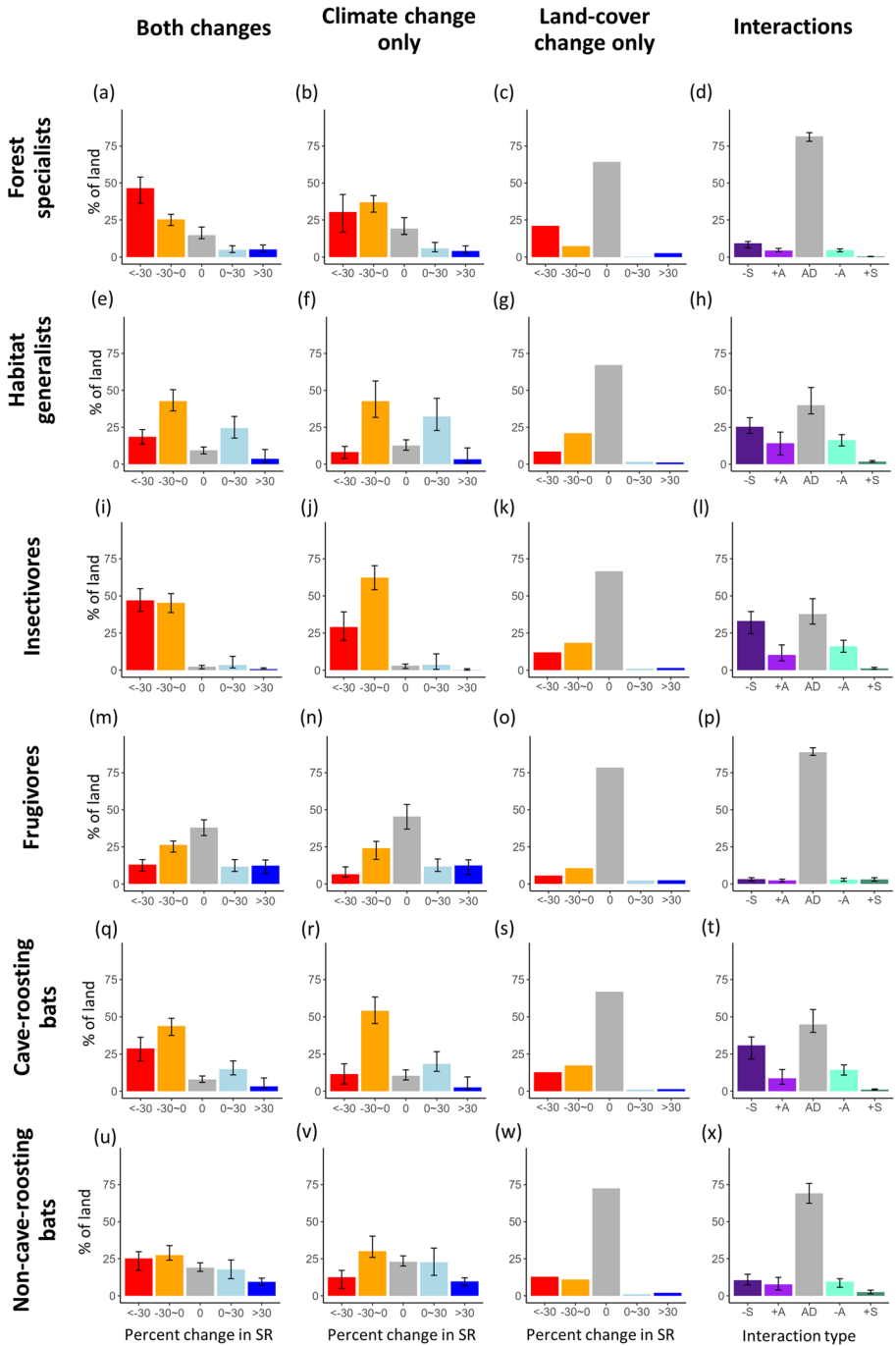
Discussion

This study showed that projected future climate and land-cover changes would have profound and negative impacts on the potential range size of individual bat species and species richness across Vietnam. Our model predictions indicated that both environmental changes would individually result in predominantly negative effects. When these changes occurred simultaneously, their interactions would exacerbate the impacts by primarily enhancing the negative effects or mitigating the positive effects of each change. Therefore, the combined effects of climate and land-cover changes were predicted to lead to range contractions in two-thirds of the species and a loss of species richness in almost three-fourths of the land area in Vietnam by the 2050s. These negative impacts would be particularly significant for forest specialists, insectivores and cave-roosting species, as well as in the forests and grasslands of northern and southern Vietnam. The considerable variations in bats' responses, especially to climate change, among different species and functional guilds, as well as across geographic areas, pose a challenge for conservation efforts. It is clear that a “one-size-fits-all” strategy is not applicable in this context. However, the species-specific and spatially-explicit impacts predicted by this study provide valuable insights that allow for targeting more vulnerable species and geographic areas, as well as developing strategies to address more manageable and less uncertain impacts. Therefore, incorporating not only the individual effects of climate and land-cover changes but also their interactive effects into impact assessment and conservation planning for bats is of utmost importance.

Differences in the individual effect of climate and land-cover changes

Consistent with previous studies (Bailey et al. 2017; Hughes et al. 2012; Zamora-Gutierrez et al. 2018), our findings demonstrate generally negative impacts of climate and land-cover changes on bats. However, our model predictions revealed that the effects of the two environmental changes differ in both direction and magnitude. While both changes were predicted to have an overall negative effect on bats, approximately one-third of the species would experience a potential range expansion, and one-fourth of the land area in Vietnam would gain species richness as a result of projected climate change (Figs. 3 and 4). In contrast, the effects of land-cover change would predominantly be negative.

Previous studies have also reported mixed impacts of climate change on bats (Diengdoh et al. 2022; Thapa et al. 2021) and other taxa (i.e. Currie 2001; Hamann and Wang 2006; Iverson and Prasad 2001), with some species experiencing negative effects while others showing positive responses. This variation is likely due to



interspecific differences in climate preference or tolerance (Rebello et al. 2010). In contrast, forests are critical habitat for bats, providing shelter, foraging opportunities, and reproductive spaces (Hayes et al. 2007). In this study, all 81 modeled species use forest as at least part of their primary habitat, and forest cover emerged as one of the most important factors influencing bat distributions across species (Fig. S8). Given that forest cover in Vietnam is projected to decrease from 39.1% to 2010 to 26% and 23.2% in 2050 under moderate and extreme emission scenarios, respectively (Fig. S13), the predominantly negative effect of land-cover change is not surprising (Figs. 3 and 4). However, it is important to note that the difference in the direction of effects does not necessarily imply that land-cover change would have a more negative impact on individual bat species compared to climate change. Consistent with other studies (Lemoine et al. 2007; Newbold 2018), we found that for species negatively affected by climate change, the effect would be stronger than that resulting from land-cover change (Fig. 3b, c). Furthermore, while climate change is anticipated to impact nearly the entire country, land-cover change would only affect approximately one-third of the country. Therefore, climate change is expected to have broader impacts over a larger area compared to land-cover change.

Interactive effects of climate and land-cover changes

Our study provides the first evidence that the interactions between climate and land-cover changes would have significant impacts on bats' distributions and richness patterns, consistent with previous findings on other taxa (Mantyka-Pringle et al. 2012; Santos et al. 2021). However, unlike previous studies that typically show a dominance of synergistic interactions between the two environmental changes (Cote et al. 2016; Segan et al. 2016), we found that antagonistic interactions would also be common or even more prevalent than synergistic interactions in their effects on bats' potential range size (Fig. 3g). The inconsistent findings may be due to variations in species' responses among taxa (Mantyka-Pringle et al. 2012), geographic regions (Segan et al. 2016), or a combination of both (Mantyka-Pringle et al. 2015). However, the main reason could be the different approaches used to classify interaction types.

Many previous studies simply classified an interaction as synergistic if the combined effect was more negative than the sum of (or even one of) the individual effects (e.g., Marshall et al. 2018; Piessens et al. 2009; Radinger et al. 2016), assuming that the individual effects were negative. If we had used that classification approach (i.e., classifying $-S$ and $+A$ as synergistic and $+S$ and $-A$ as antagonistic effects), we would have observed a dominance of synergistic effects (Fig. 3g and 4h). However, since the effects of the environmental changes, particularly climate change, on biodiversity are not always negative, as demonstrated by this and other studies (Currie 2001; Hamann and Wang 2006; Thapa et al. 2021), we believe that examining interactive effects with explicitly accounting for the direction of individual effects (Piggott et al. 2015) is a more appropriate and more informative approach. One example is the predicted changes in species richness in northern Vietnam (Fig. 4), where the two environmental changes would synergistically enhance their negative individual effects while antagonistically mitigate positive effects, leading to an overall negative interactive effect. Without accounting for the effect direction, previous approaches would incorrectly classify the antagonistic interactions as synergistic ones.

Different responses of functional guilds to the environmental changes

Our findings indicate that the impacts of climate and land-cover changes vary among functional guilds. Consistent with previous studies on bats (Gonçalves et al. 2021) and other taxa (Roberts et al. 2011), we found that habitat specialists are more sensitive to environmental changes compared to generalists due to their narrower niche (Newbold et al. 2018; Staude et al. 2020) and/or stronger association with specific habitat or resources (Novella et al. 2022). The higher vulnerability of forest specialists to climate and land-cover changes, as observed in this study, is likely attributable to their narrower climatic niche and their dependence on diminishing forests in Vietnam, respectively. The negative individual effects on forest specialists were predicted to be further amplified when the two changes occurred simultaneously. In contrast, the interactive effects would be less negative on habitat generalists. This is likely because the climate was projected to become less suitable for most bats in forests and grasslands, while becoming more suitable in farmlands and built-up areas in the future (Fig. 4b).

Similarly, we also found that insectivorous bats would be more vulnerable than frugivores to the two environmental changes, especially to their interactive effects. The negative individual effects on insectivores would mostly be enhanced, while those on frugivores would be mitigated. Insectivorous bats, especially aerial hawking species, are recognized to be highly sensitive to climate change, because they are dependent on food resources that are spatially and temporally variable and are sensitive to temperature changes (Sherwin et al. 2013). Furthermore, morphological differences between the two dietary guilds could be another reason for their different responses to environmental changes. Old-world insectivorous bats usually have a smaller body size and lower wing loading than old-world frugivorous bats (Norberg 1994; Wilson et al. 2019). Although the body size and wing loading of a species are generally positively correlated with range size (Gaston and Blackburn 1996; Jenkins 1981), our results did not show an association between the range size of the species and its predicted changes (Fig. 3). However, smaller species are less tolerant to starvation, making them more sensitive to changes in habitat or food availability (Blackburn and Hawkins 2004). Additionally, species with lower wing loading tend to have more limited dispersal ability, which could make them vulnerable to climate change due to reduced capacity to track suitable environments (Varzinczak 2020). Finally, it is also possible that the different responses are associated with niche breadth, as 11 out of the 12 frugivores studied are habitat generalists (Table S2).

Our results suggested that the choice of roosting site can influence bats' responses to the two environmental changes, specifically in terms of changes in species richness across space, but not in species range size (Figs. 5q–x and 6q–x). This implies that the difference observed could be related to range shifts. Under projected climate change, both cave-roosting and non-cave-roosting species were predicted to increase in species richness in the farmlands along the coast from the Red River Delta to the North Central Coast. However, the increase was more pronounced for non-cave-roosting species (Fig. S14). Furthermore, while most areas in the Northeast and Northwest were predicted to experience a loss of cave-roosting species, some of these areas would see an increase in non-cave-roosting species in the future (Fig. S14). This pattern may be attributed to the potential for non-cave-roosting species to shift their ranges in response to suitable climates, whereas cave-roosting species are limited to the areas with suitable caves (Scheel et al. 1996). It is also possible that non-cave-roosting species are more sensitive to climate change as they are less insulated from climatic fluctuations compared to cave-roosting bats (Turbill 2008).

While further research is necessary to fully understand the mechanisms driving the differential responses of functional guilds to the environmental changes, these differences can have significant implications for the ecological functions and ecosystem services provided by bats in Vietnam. For example, the high vulnerability of insectivorous bats may lead to a decline in the pest suppression services they provide in the future. Insectivorous bats have been recognized for their crucial role in suppressing pests in agricultural systems, making essential economic contributions both locally and globally (Boyles et al. 2013). Given that agriculture is a vital sector in Vietnam's economy (Duong 2020), the predicted loss of species richness among insectivorous bats in farmland areas, particularly in the Mekong River Delta (Fig. S14), could result in significant agricultural and economic losses for the country. This highlights the urgent need for conservation strategies to mitigate these potential impacts and preserve the valuable services provided by bats.

Conservation implications

Our results emphasize the urgent need to protect bats in Vietnam, as the majority of species are likely to experience negative impacts from climate and land-cover changes by the mid-century. It is important to note that our predictions may underestimate the severity of the impacts, because our models did not consider other threats to bats, such as hunting or collisions with wind turbines (Arnett et al. 2016; Son et al. 2009), and assumed that bats would fully occupy all suitable habitats in the future.

The complex and diverse interactions between climate and land-cover changes revealed in this study highlight the necessity of integrating both individual and interactive effects into bat conservation planning in Vietnam. Particularly, the substantial variations in the effects among species and across the country underscore the importance of species-specific and spatially explicit information to develop effective conservation strategies. For example, conservation efforts may yield greater cost-effectiveness when focused on species or regions affected by synergistic interactions between the two environmental changes, rather than those influenced by antagonistic interactions (Cote et al. 2016). Synergistic interactions allow conservation actions aimed at mitigating the negative effects (or enhancing the positive effects) of one change to also address the negative effects (or enhance the positive effects) of the interactions. Synergistic interactions also allow resources allocated to manage changes that are relatively manageable and predictable (i.e., with low uncertainty; Ghedini et al. 2013; Strain et al. 2015). In the context of bat conservation in Vietnam, halting land-cover change, particularly deforestation, is expected to be a more cost-effective strategy compared to mitigating the impacts of climate change. This is because land-cover change has more consistent effects across species and space, and affects smaller regions (around one-third of the country). Addressing land-cover change can also be facilitated through conventional and well-established approaches such as establishing protected areas and implementing payments for ecosystem services (Geldmann et al. 2013; Tuanmu et al. 2016). Implementing this strategy would be particularly effective in northern Vietnam, where negative effects of land-cover change and negative synergistic interactions between the two environmental changes are expected to be more dominant (Fig. 4c and d). Importantly, only a small portion of this area is currently protected (Fig. 1b), underscoring the significance of managing land-cover changes outside protected areas for effective bat conservation.

For species primarily impacted by climate change or antagonistic interactions between climate and land-cover changes, addressing land-cover change alone may be insufficient

or not cost-effective to protect them. In such cases, an alternative strategy would be to enhance their adaptation to expected climate change. Although habitat connectivity was not explicitly included in our models, enhancing habitat connectivity has proven to be effective in assisting species in adapting to climate change by allowing them to track suitable climates or maintain metapopulation persistence (Heller and Zavaleta 2009). Considering the projected increase in climatic suitability for bat species along the eastern coast and in the Central Highlands (Fig. 4b), it becomes crucial to prioritize habitat connectivity improvement through habitat restoration and corridor establishment within and around this region. The Central Highlands, which is expected to sustain high bat diversity in the future (Fig. 1c), could potentially serve as a refuge for bats. Establishing corridors that connect the Central Highlands with habitats in other regions would be essential. This strategy holds particular significance for the conservation of forest specialist bats and insectivorous bats, as their richness patterns are anticipated to be significantly and adversely affected by climate change (Fig. S14). Regarding cave-roosting bats, whose distributions are limited to regions with suitable caves, the priority should be placed on protecting these caves from human disturbances and maintaining or enhancing habitat connectivity among them (Furey and Racey 2016).

It is important to note that before implementing specific conservation actions, further studies incorporating information on the population status, species composition of bats, habitat characteristics, and socioeconomic conditions of local communities in those areas are necessary. Additionally, considering the uncertainties associated with future predictions and the assumptions underlying species distribution modeling (Beale and Lennon 2012; Carvalho et al. 2011), it is imperative to adopt adaptive conservation approaches, which involve continuously evaluating and adjusting current strategies based on new information and knowledge (Lawler 2009).

Conclusions

Climate and land-cover changes are among the major threats for many taxa (Newbold et al. 2015; Parmesan 2006;). However, the two changes are seldom examined simultaneously and information on their interactive effects is rarely included in conservation planning (Cote et al. 2016; Oliver and Morecroft 2014). We presented the first study on how projected climate and land-cover changes may interactively and profoundly reshape bat species distributions and species richness patterns. We also highlighted the importance of the species-specific and spatial-explicit information on the individual and interactive effects of the two environmental changes in conservation planning and provided specific suggestions for bat conservation in Vietnam. Multiple environmental changes are affecting and will continue to affect many other taxa interactively (Mantyka et al. 2012; Radinger et al. 2016). Understanding the interactions and examining the interactive effects of multiple stresses would be a critical step in biodiversity conservation in the face of global changes. The findings of this study, along with the developed approaches, particularly the integration of species distribution modeling and the directional interaction classification system (Piggott et al. 2015), have broader applicability in the development of conservation strategies for other taxa and biodiversity as a whole.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10531-023-02709-5>.

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Author contributions LQT and MNT conceived the study, with input from JCCH. VDT, NTL, NTS, HTT, VTT, MNT, GC, TG, and NTV provided unpublished bat occurrence records. LQT compiled data with assistance from JCCH, conducted analyses with assistance from TAT in GIS, and worked under the supervision of MNT. LQT and MNT drafted the manuscript and all authors contributed to the final manuscript.

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Data availability All data are available from the sources cited in the Methods or from the authors upon request.

Declarations

Competing interests The authors declare no competing interests.

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