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Karst as an abiotic driver of François' langur distribution, with predictions for biological communities on karst under climate change

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Abstract

Ecological niche models (ENMs) can project changes in species' distributions under climate change and thus inform conservation efforts and further our understanding of patterns of change. Predictions of species' distribution shifts under climate change in topographically and geologically complex landscapes, such as karst landforms, should be improved by better integration of non-climate abiotic variables, such as karst geology or habitat structure, into model projections. We built ENMs for one of the limestone langurs, a group of leaf monkeys adapted to forests on the Sino-Vietnamese limestone karst landform. We collected occurrence localities for François' leaf monkeys (*Trachypithecus francoisi*) and thinned them to avoid sampling bias. We included as environmental parameters a global dataset for karst geology and 19 bioclimatic variables derived from monthly temperature and precipitation at 30 arc-second resolution. ENMs including karst geology and climatic variables outperformed and differed spatially from climate-only models. Across six future-climate scenario projections, the optimal karst+climate model differed from the best climate-only model and predicted more spatial overlap with karst in the future, a contraction in total area of suitable habitat by the 2070s, and a small loss in the amount of suitable habitat in existing conservation areas. This study shows the importance of considering other abiotic factors beyond climate in projections of suitable habitat under climate change for species in complex landscapes. Because our results show that karst and climate interact to explain the distribution of a karst-adapted species, the results also suggest that, under climate change, these interactions are likely to produce altered networks of species into novel biological communities. Finally, our results support the need for conservation of limestone habitats and cross-border collaboration to maintain refuges and movement connectivity for endangered species in the face of climate change.

Highlights

- Climate change may result in shifts in species' distributions, leading to changes in biological communities and increasing the likelihood of local and global extinctions.
- High endemic biodiversity coincides with known and unknown biogeomorphological feedbacks and interactions in topographically and geologically complex landscapes like karst landforms, which can complicate predictions of species' distribution shifts under climate change.
- We built and projected distribution models for *Trachypithecus francoisi*, a leaf monkey adapted to forests on the Sino-Vietnamese limestone karst landform, to show that models combining karst geology and climate as drivers outperformed models built only with climate data, with differing projections for distribution shifts under future climate change.
- Including karst geology or other non-climate abiotic variables that approximate microclimate heterogeneity will be important for distribution shift predictions for other species in karst landforms and other complex landscapes.
- Urgent, cross-border collaborations are likely needed for the conservation of the endangered biodiversity of the Sino-Vietnamese Karst Landform in the face of climate change.

Keywords: climate refugia, conservation planning, cross-border conservation, ecological niche modeling, range shift, species distribution modeling, *Trachypithecus francoisi*

Introduction

Climate change is likely to cause shifts in biological communities as novel climates appear, major biomes are redistributed, and annual temperatures increase (Parmesan and Yohe 2003, Corlett 2012, IPCC 2013). There are numerous predicted negative effects from redistributions of biodiversity and climate change on human well-being (Pecl et al. 2017). Many studies to date focus on documenting observed impacts of climate change on species' distributions and characteristics (e.g. Rosenzweig et al. 2008) or predicting future impacts including vulnerability and extinction risk (e.g. Thomas et al. 2004, Li et al. 2013). For example, climate change is expected to shift species' distributions and increase the likelihood of local and global extinctions (Parmesan et al. 1999, Pounds et al. 1999) as areas suitable for species' survival contract or expand (Huntley et al. 2008, Thomas 2010). Studies also suggest cascading effects of redistributions, due to changes in species interactions or community assembly or structure, towards impacts on entire guilds (e.g. Brambilla et al. 2020).

One strategy proposed to mitigate the negative effects from predicted redistributions is to identify, understand, and conserve climate refugia, or regions where hotspots of endemism coincide with low levels of climatic oscillation (Keppel et al. 2012, Harrison and Noss 2017, Morelli et al. 2020). Recent studies identify the importance of microclimate and climate microrefugia, or areas where species may persist locally due to more moderate changes in climate compared to a larger surrounding region (e.g. Keppel et al. 2012, Hannah et al. 2014, Harrison and Noss 2017). Factors such as cool mountaintops (e.g. Ohlemüller et al. 2008), fine scale topographic or geological variation (and associated shading, e.g. Keppel et al. 2017), and other 'small natural features' (Fitzsimons and Michael 2017, Hunter 2017) influence microclimate conditions like wind speed, humidity, short- and long-wavelength radiation, and soil moisture. Rarely are microclimate conditions explicitly captured in existing models of species' distribution shifts under past or future climate change (Franklin 2013, Keppel et al. 2017). In the few cases where they are captured, however, they tend to be important. For example, dolines or karstic depressions (sinkholes) can be climatic microrefugia for cool-adapted plants in Europe (Bátori et al. 2017). Thus, predictions of redistributions of species under climate change could be improved by better integration of microclimate information or non-climate abiotic variables, such as geology, solar radiation, soil depth, topography and habitat structure, that likely interact to produce varied microclimate conditions (e.g. Brown and Yoder 2015, Keppel et al. 2017, Suggitt et al. 2018).

Further, there is a need to improve understanding of how species' distributions will respond to climate change in topographically and geologically complex landscapes, such as karst landforms, where high endemic biodiversity coincides with known and unknown biogeomorphological feedbacks and interactions. Karst landforms and hydrological systems form through the dissolution of porous, soluble bedrock, namely

limestone (Gillieson 2005, Ford and Williams 2007). Karsts cover approximately 11% of the world's land surface and, including subterranean hydrological systems, more than 14% of global land areas (Williams 2008). Although microclimate conditions are highly variable and patchy, in general karsts are harsh and dry, with rainwater draining quickly, and thin, alkaline soil that is poor in nutrients except metal ions such as calcium and magnesium (Clements et al. 2006, Sterling et al. 2006, Chung et al. 2014).

Forest formations on karsts correlate with microendemic distributions of taxa and high endemic species richness (Clements et al. 2006, Su et al. 2017, Grismer et al. 2020). While climate plays a major role in shaping communities and species' distributions (e.g. Kraft and Ackerly 2010, Graham et al. 2012, Rowan et al. 2016), there are several unique geomorphological and hydrogeological characteristics of karst landscapes and complex biotic-abiotic interactions that likely combine to generate high endemic biodiversity in karst forests (Goldscheider 2012, Bárány-Kevei and Kiss 2016, Phillips 2016). Karsts were also likely refuges for species during past glacial cycles because of cave shelters and heterogeneous, diverse microclimates (Soto-Centeno et al. 2015, Mammola and Leroy 2018). Thus, information about karst could greatly influence and likely improve predictions of karst specialist species' redistributions in response to climate change.

Ecological niche models (ENMs; Peterson et al. 2011) estimate environmental suitability for a species using associations between species' occurrence records and environmental variables (Franklin 2009, Peterson et al. 2011). ENMs are widely used in conservation assessments and planning (e.g. Blair et al. 2012), to understand evolutionary processes (e.g. Bett et al. 2012, Blair et al. 2013), and to predict species distribution shifts in response to climate change (Keith et al. 2008, Fordham et al. 2012, Wong et al. 2013). There is a great deal of attention to advance ENM methods to better account for key issues such as sensitivity to sampling bias, sample size, parameterization, and evaluation (e.g. Bean et al. 2012, Merow et al. 2013, Muscarella et al. 2014, Galante et al. 2018). In addition to these advances, and as mentioned above, ENM-based projections of changes in species' distributions under climate change in topographically and geologically complex landscapes such as karst landforms would be further improved by better integration of non-climate abiotic variables, such as karst geology. Inclusion of such variables should serve to approximate the varied microclimate conditions and geomorphological or hydrogeological characteristics of these complex landscapes, which likely play a role in mediating or even buffering species' responses to climatic or other environmental changes (Soto-Centeno et al. 2015, Mammola and Leroy 2018, Suggitt et al. 2018).

Here, we build an ENM for an endangered species of 'limestone langur' native to the Sino-Vietnamese karst landform (southern China [Guangxi, western Guangdong, southern Guizhou, and southeastern Yunnan] and northern Vietnam [Tuyen Quang, Thai

Nguyen, Lang Son, Ha Giang, and eastern Yen Bai, Lao Cai]). This is one of the largest karst landforms of pure carbonate bedrock and is considered a model system for karst studies (Sweeting 1978). The limestone langurs are a group of primates whose habitat comprises Southeast Asian karst formations. This group falls within the genus *Trachypithecus* (Primates: Cercopithecidae) Reichenbach, 1862, which consists of about 17–20 species with diversification dated to the early Pleistocene and one monophyletic sub-clade of 5–7 species that diverged in the mid-Pleistocene, all currently limited to karst habitats. The limestone langurs are also referred to as the *T. francoisi* group (Groves 2001, Osterholz et al. 2008, He et al. 2012), named for *T. francoisi* or the François' langur (de Pousargès 1898, Dào 1970). Members of the *T. francoisi* group are known to sleep in karst caves and easily locomote on steep vertical karst cliffs (Huang et al. 2004, Workman 2010).

A dramatic population decline for *T. francoisi* was documented recently (Hu et al. 2004, Li et al. 2007), and the IUCN Red List recognizes all but one of the 16 *Trachypithecus* species as threatened with extinction; *T. francoisi* and the other limestone langurs are considered highly endangered and priorities for national conservation action plans (e.g. Jiang et al. 2016, MARD 2017, IUCN 2020). While one study to date has projected a climate-based ENM for *T. francoisi* under future climate change in Vietnam (Vu et al. 2011), it remains unclear how climate change might affect the overall distribution and potential continued decline of *T. francoisi* or the other limestone langurs in the context of their likely ecological specialization to a specific geology.

The ENMs we build here for *T. francoisi* include karst geology as an abiotic driver in addition to climate to explore the importance of karst geology in predicting the current distribution of this species, and in estimating the potential impacts of climate change on future climatically suitable habitat. We summarize our results to provide recommendations for policy-based planning and management actions to support the conservation management of this highly endangered species, the other limestone langurs, and other karst-specialist or dependent species. We also discuss how our results contribute to broader understanding of climate change effects and drivers of endemism in this subtropical, topographically complex, and highly heterogeneous region.

Materials and Methods

We collected 211 occurrence localities from the literature for *T. francoisi* (Fooden 1996, Nadler et al. 2003, Hu et al. 2004, Zhou et al. 2006, Li et al. 2007, Yang et al. 2007, Duckworth et al. 2010, Han et al. 2013, Nguyen et al. 2014, Niu et al. 2016) and from the Guangxi Forestry Inventory and Planning Institute (Appendix S2 Table S1). We removed three points that we felt were unreliable because they were only accurate to the nearest half-degree and thinned the remaining occurrence localities to reduce sampling bias and spatial autocorrelation effects using the R package

SpThin (Aiello-Lammens et al. 2015) with a thinning distance of 10km for a final dataset of 131 localities. We also compiled information on *T. francoisi* recorded presence in four other nature reserves in Guizhou and Chongqing Provinces but could not find precise occurrence locality information for these areas. Thus, we held back this information in model training and discuss in our results whether the ENM built on the occurrence locality data predicted potential *T. francoisi* presence in these four reserves.

We built two types of ENMs for *T. francoisi* using two sets of environmental input variables: a set of climatic variables only (“climate-only”) and a set that included karst geology along with climatic variables (“karst+climate”). As climatic variables for the ENM we used the 19 continuous bioclimatic variables derived from monthly temperature and precipitation values at 30 arc-second resolution available from worldclim.org (Fick and Hijmans 2017). For future climate projections we used six future climate model and socioeconomic pathway projections including two global climate models BCC-CSM2-MR and MIROC6 for each of three Shared Socio-economic Pathways or SSPs from the 2021 IPCC 6th assessment report CMIP6: SSP2-4.5, SSP3-7.0 and SSP5-8.5 (at 2.5 arc-minute resolution, the highest resolution available at the time of analysis; Fick and Hijmans 2017).

We used the World Map of Carbonate Rock Outcrops v3.0 (2016 update to Ford and Williams 2007) to create a categorical karst data layer. The distribution of carbonate rock outcrops can approximate karst landform geology because most carbonate rocks are susceptible to karstification (Ford and Williams 2007, Mammola and Leroy 2018). To create our categorical environmental layer to approximate karst habitat, we added to the carbonate rock outcrop dataset a 20km buffer to account for inconsistent resolution of the outcrop dataset across countries and potential errors; two “outlier” *T. francoisi* occurrence localities from Lang Son Province in Vietnam were more than 70km away from the nearest karst outcrop in the Ford & Williams (2007) dataset. Co-authors who are familiar with the area in Vietnam (MEB, MDL) confirmed that there is indeed karst in Lang Son in small patches near the border with Cao Bang Province; as other studies have suggested, these karst patches were likely not captured well by the generalization methods used by the global dataset because of their small size (Chen et al. 2017). We assumed the distribution of karst does not change in the near future and thus used the same karst dataset to predict both current and future suitable habitat for *T. francoisi*.

We then generated ENMs in R using the maximum entropy algorithm in Maxent v 3.4 (Phillips et al. 2017). To minimize the effects of sampling bias on model training, we constrained the background model training region to a 5-degree buffered area (roughly 1050 km) around a minimum complex polygon containing the thinned occurrence localities. We sampled 10,000 background localities from within this region for model training. To minimize overcomplexity and overfitting of the model, we tuned models using

ENMeval (Muscarella et al. 2014) and tested a range of regularization multiplier setting values (from 0.5 to seven by intervals of 0.5) and combinations of feature classes (linear, linear + quadratic, linear + quadratic + hinge, and hinge features). This resulted in 56 models for each variable set from which to select the optimal parameter settings for the model. We employed a geographic partitioning (block method; Muscarella, et al., 2014) validation approach for withholding testing data (Shcheglovitova and Anderson 2013) and selected the optimal model based on common model performance metrics, specifically the lowest average evaluation omission error, then highest average evaluation test area under the receiver operating characteristic curve (AUC). Optimal models were also evaluated using their AICc score (Akaike Information Criterion small sample size corrected) and the number of parameters included in the final model, which provide information on model complexity. We projected the optimal model for each variable set (karst+climate and climate-only) to the six future climate model and socioeconomic pathway projections noted above.

For visualization, we projected models using the complementary log-log transformation (cloglog). Cloglog has a stronger theoretical justification than the logistic transformation and is derived from an interpretation of Maxent as an inhomogeneous Poisson process (Phillips et al. 2017). We also generated binary model projections (thresholded models) for the current and future projections to calculate the mean and projected range of change in suitable habitat as well as the proportion of change in suitable habitat within in conservation areas. Models were thresholded using the equal training specificity-sensitivity threshold of the cloglog projection. Additionally, we removed predicted areas that exhibit unreasonably low (most dissimilar) multivariate environmental similarity surface (MESS) values. We calculated overlap with conservation areas using the IUCN WCPA database (UNEP-WCMC, IUCN 2020). We also calculated the distance of the shift in the centroid of the thresholded climatically suitable habitat from current to future ENM projections. We compared the spatial overlap between karst+climate and climate-only model projections using Schoener's *D*-value (Schoener 1968, Warren et al. 2008).

Results

The optimal model for the karst+climate ENM had a regularization multiplier of 5 and linear + quadratic feature classes (average test omission rate at the 10% training presence threshold = 0.077, average evaluation AUC = 0.942, and delta AICc = 58.97). The optimal model for the climate-only ENM had a regularization multiplier of 2 and linear + quadratic + hinge feature classes (average test omission rate at the 10% training presence threshold = 0.093, average evaluation AUC = 0.940, and delta AICc = 38.82). Following the model performance criteria as laid out in the methods (omission rate and AUC), the optimal karst+climate ENM performed better and was also less complex (10 parameters) than a model trained just with climate variables (30 parameters— see Appendix S2, Table S2).

The karst+climate ENM also differed spatially from the climate-only model (Schoener's *D* = 0.77) and predicted 10% more spatial overlap with karst areas in the current climate (Fig. 1). We also note that 88% of the *T. francoisi* localities are within 20 km of the original (unmodified) global carbonate rock outcrop dataset (Fig. 1 and see Appendix S1).

Both final ENMs successfully predict the current known range of *T. francoisi* but also overpredict outside the known range, especially to the east (Fig. 1). The variables used in the optimal ENMs (with non-zero lambda values) are presented in Supplementary Table S2 (Appendix S2). Models were thresholded at the equal training sensitivity-specificity (ETSS) threshold to create binary predictions. The ETSS threshold for climate-only models is 0.2541, and for the karst+climate model; 0.2889. Models successfully predicted another area in Vietnam (Lam Binh District, Tuyen Quang Province; Thach 2011) known to have *T. francoisi* but not included in the model training dataset. However, the models did not predict the four additional nature reserves in Guizhou and Chongqin Provinces (Kuankuoshui National Nature Reserve, Dashashe Nature Reserve, Jinfoshan Nature Reserve, Yezhong Nature Reserve) with recorded *T. francoisi* presence, suggesting that the predictive ability of models could be further improved by the inclusion of additional training data or improved environmental variables.

Fig. 2 shows the overlap across six future climate model and socioeconomic pathway model projections for the optimal karst+climate model. Karst+climate model projections show a small contraction in total area of suitable habitat by the 2070s and a small loss in the amount of suitable habitat in existing conservation areas (Table 1). Models predict a northerly shift in centroid location of most suitable habitat due to the predicted range contraction (Fig. 2, Table 1). By contrast, climate-only model projections predict a much larger contraction in total area of suitable habitat in the future along with a large northerly shift (Table 1, Appendix S2 Table S3). Overlap between the karst+climate and climate-only projections under future climate scenarios was less than in the current climate (Schoener's *D* ranging from 0.503 - 0.683), with karst+climate models predicting on average more than four times the amount of spatial overlap with karst under future scenarios than climate-only projections, and smaller centroid shifts (Table 1, Fig. 2, Appendix S2 Fig. S1).

Discussion

Karst+climate ENMs outperformed climate-only ENMs in their projections of current *T. francoisi* distribution and predicted 1.5 times more spatial overlap with karst areas. The optimal karst+climate ENMs showed lower omission rates and higher discriminatory ability between true presences and background. Including relevant abiotic interactors in ENM can lead to more realistic niche characterizations (Anderson 2017) and more accurate predictions. In projections under future climate scenarios, the karst+climate model projections also differed from

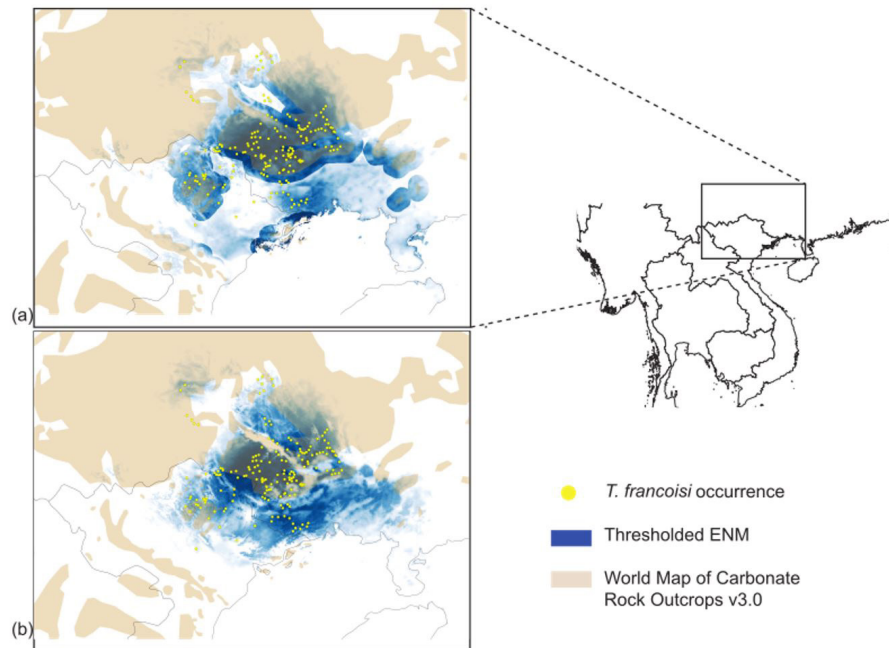


Figure 1. Modeled suitable habitat for the current climate for *Trachypithecus francoisi* for the karst+climate variable set (a) and the climate-only variable set (b). Yellow circles represent occurrence data used to train the model and brown polygons represent the carbonate rock outcrop dataset used to represent karst in models (Ford and Williams 2007). Darker blue indicates higher modeled suitability.

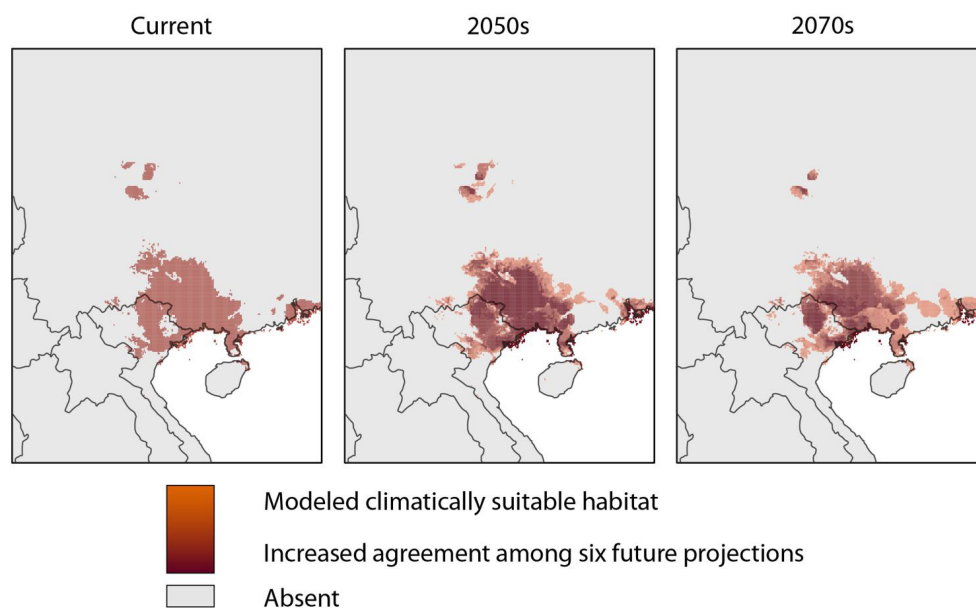


Figure 2. Karst+climate ENM projections for *Trachypithecus francoisi* for the current climate and future projections to the 2050s and 2070s with darker red shades indicating increased agreement (overlap) across six future climate model and socioeconomic pathway projections (two global climate models BCC-CSM2-MR and MIROC6 for each of three Shared Socio-economic Pathways or SSPs from the 2021 IPCC 6th assessment report CMIP6: SSP2-4.5, SSP3-7.0 and SSP5-8.5).

the climate-only projections, predicting more spatial overlap with karst in the future, less contraction, and less of an overall shift (Table 1, Fig. 2, Appendix S2 Fig. S1). Both our karst+climate and climate-only projections differed from the results of a previous study that used only climate variables and a different ENM algorithm (BIOCLIM) to project the future effects of climate change for the *T. francoisi* population in

Vietnam (Vu et al. 2011). Vu et al. (2011) found that *T. francoisi* distribution in Vietnam may expand overall and shift north and west under future climate change. In contrast, both our karst+climate and climate-only ENMs point to a contraction in total area of suitable habitat by the 2070s and a loss in the amount of suitable habitat in conservation areas (Table 1). While both studies predict a northerly shift in *T. francoisi*

Table 1. Summary of future projected changes (mean and range across six different climate model and socioeconomic pathway projections) in ENM-modeled suitable habitat for *Trachypithecus francoisi* based on models that incorporate karst+climate (above) and only climate variables (below) in model training.

Model type	Time-frame	Change in suitable habitat in conservation areas	Total projected suitable habitat change (km ²)	Projected amount of shift in suitable habitat (km)	Overlap with karst
Karst+ climate	2050s	-0.08% (-0.60 to +0.57)	+53,000 (-173,000 to +12,000)	29.3 (8.0 to 150)	3.35% (2.69% to 4.80%)
	2070s	-0.67% (-2.99 to +0.03)	-101,000 (-141,000 to +230)	56.8 (13.2 to 93.6)	2.74% (1.25% to 3.97%)
Climate- only	2050s	-0.54% (-1.72 to +0.10)	-180,000 (-234,000 to -12,000)	118.3 (91.9 to 182.3)	1.01% (0.55% to 2.18%)
	2070s	-1.77% (-6.17 to -0.31)	-209,000 (-240,000 to -162,000)	142.9 (93.7 to 230.6)	0.59% (0.05% to 1.5%)

range, the major differences in our predictions of expansion versus contraction are likely due to the improved dataset and model tuning procedures employed in our study. Overall, our results confirm that limestone karst geology informed ENM model training and projections for the François' langurs towards higher performing models that are useful for climate change mitigation and adaptation planning.

These results also contribute to ongoing debate as to whether the perceived relationship between the limestone langurs and karst habitat may be subject to historical bias; meaning, these langurs may have been restricted to limestone only recently due to anthropogenic activity rather than ecological requirements (Li and Rogers 2005, Workman 2010). Others also mention anthropogenic disturbance as a possible alternative explanation for mammal species' current distributions on karst (Furey et al. 2010, Latinne et al. 2013). However, new analysis of limestone langur genomes including the full genome of *T. francoisi* shows evidence of functional gene evolution related to calcium signaling (Liu et al. 2020). This finding, combined with behavioral and plant physiological evidence, supports that the limestone langurs are ecologically specialized primates adapted to significantly higher levels of natural calcium intake; limestone langurs drink water from karst holes that contain high concentrations of calcium and other minerals (Huang and Li 2005, Hu 2007, Liu et al. 2016), have been observed to lick limestone rock (Li et al. 2003, Zhou et al. 2006, Liu et al. 2020), and consume leaves from karst-adapted plants that exhibit significantly higher levels of calcium compared with other plant communities (e.g. *Lonicera confusa* Wu et al. 2011, Jin et al. 2018).

While anthropogenic activity has and continues to affect limestone langur habitat, our results add to the growing support that *T. francoisi* does have ecological specialization to karst geology, and thus, the addition of karst geology as input variables will likely to be important for modeling other members of the limestone langur clade. In addition, the conservation of

limestone karst is essential for the future persistence of these and likely many other karst-specialized groups. Urgent communication to conservation managers, practitioners, and government decision-makers of the importance of cross-border collaboration for the conservation of limestone karst habitats is warranted given increasing threats to limestone habitats for cement mining (Clements et al. 2006).

Our results indicate that karst and climate interact to explain the distribution of karst-adapted species. Because karst also harbors unique communities of interacting species (Clements et al. 2006), karst and climate likely interact to predict changes in networks of species. Karst topography extends the temperature and moisture gradient available in the landscape, and increases microclimate heterogeneity at various scales, which can facilitate a buffering effect to reduce extinctions during periods of climate change (Soto-Centeno et al. 2015, Suggitt et al. 2018). Higher microclimate diversity can also relate to high speciation rates and/or stronger interspecies interactions due to topographical and geological confinements that facilitate niche partitioning (Rohde 1992, Brown 2014). Thus, microclimate processes could explain the high endemic richness of karst biological communities and lead to predictions of how much future climate change will influence not just species' distributions, as shown here, but species' interactions and networks. For example, if climate change occurs at a rate or amplitude beyond the buffering capacity of the karst landscape, or if karst serves as a filter under climate change for one interacting species but not the other, species may have to leave karst sanctuaries and may or may not lose their supporting communities, changing biological community structure. In some cases, karst-adapted species may be too specialized to be able to survive elsewhere, and some incoming species may not be able to adapt to the karst environment quickly or lack genetic adaptations to deal with more calcium-rich and high-pH soils (e.g. calcifuges or plants that do not tolerate alkaline soil). Other generalist species, however, may be able to adapt quickly to

karst environments (e.g. Li et al. 2020). Overall, we can predict that karst will be a filter for biological communities under future climate change resulting in the breaking up and regrouping of interacting species into novel communities (Ordonez et al. 2016), in what are now highly endemic and globally important landscapes.

This study and further research in this area have the potential to generate an improved understanding of the processes by which biological communities in geologically complex landscapes respond to change. Further incorporation of microclimate or microclimate proxy variables in predictions may illuminate how karst topography may buffer climate change at micro-scales in processes that might remain unobserved at global or continental scale analyses due to scale biases and filters (Suggitt et al. 2018). While coarse-scale models such as the ones we present here often fail to identify localized effects of topography on climate, we argue that the inclusion of karst geology, even at a coarse scale, seems to help approximate where fine-scale variation may be more likely to occur. But indeed, future studies should engage in finer-scale analyses using new frameworks to integrate microclimatic data into ENMs from remote sensing instruments, in-situ climate measurements, and data on habitat 3D structure (Lembrechts et al. 2019) as these data become readily available.

Finer-scale analyses will be particularly important to help target appropriate *in-situ* conservation measures by identifying refugial locations throughout the range and providing the ability to inform adaptive management through dynamically updated model predictions. In addition, development of new technologies to facilitate microclimate and other measurements (e.g. Gillingham et al. 2012) for locally-derived high resolution input variables would enable more robust incorporation of microclimate and small features into ENMs. For our study, such technologies could improve upon the coarse scale carbonate outcrop dataset used, as discussed in the Methods. Given the small and fragmented remaining populations of *T. francoisi*, fine-scale dynamic predictions might be best informed by coupling niche models with spatially explicit stochastic population models to explore the interactions of mechanisms causing population decline (e.g. Stanton et al. 2015), and with better consideration of biotic interactions (Hellmann et al. 2012). Overall, higher resolution datasets and additional modeling could improve upon the results shown here for more targeted conservation recommendations including local site monitoring plans (Dine et al. 2012).

Our study does take a key first step to enable a stronger scientific basis for conservation planning, biodiversity observation, and biodiversity monitoring on karst, which is currently lacking (Clements et al. 2008). Karst landscapes are rarely considered in conservation planning (but see Watson et al. 1997) despite hosting significant portions of an area's biodiversity, likely because of a lack of sufficient biodiversity data on karst (Grismer et al. 2020). In addition, limestone is vulnerable to overexploitation by widespread and

increasing quarrying activities throughout Vietnam and elsewhere (Clements et al. 2006). The information produced by this research will be crucial to conservation planning in Vietnam as they plan for adaptation and mitigation strategies for biodiversity on karst and elsewhere under climate change (MARD 2017). Here, we have added to the information available to inform planning, allowing the basis for more specific predictions and for the design of species management plans for conservation (e.g. Blair et al. 2012). While the future projections we report here do not account for demography, dispersal limitations, interactions among species, or other factors such as changes in human land use and thus may overestimate potential shifts, our projections also are more likely to underestimate losses (Segan et al. 2015). While there is uncertainty about magnitude of change and differences in projections across GCMs, basing decisions on agreements across a range of scenarios as we have presented here is a reasonable, conservative approach to guide management decisions (e.g. Beaumont et al. 2019). The research reported here also provides evidence to strongly support why management plans addressing synergistic anthropogenic threats must consider anthropogenic impacts on not only vegetation but geology, and recognize 'geodiversity' (Gray 2011, Record et al. 2020) in addition to biodiversity in conservation planning efforts.

Finally, our results emphasize that for many karst landscapes, including the Sino-Vietnamese karst landform that is home to *T. francoisi*, forward-thinking transboundary conservation coordination efforts will be crucial to prevent extinctions of karst-adapted species. National species conservation action plans and plans for Vision 2030 protected area strengthening and reform processes to meet Sustainable Development Goals (e.g. MARD 2017) should incorporate consideration of species' distribution changes in response to climate change across borders, including through coordinated conservation of potential movement or 'climate connectivity' corridors (Senior et al. 2019). Cross-border conservation efforts and partnerships should be encouraged and strengthened, especially through the guiding principles of stakeholder engagement and science diplomacy (CGSPSD 2011, Sterling et al. 2017).

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Author Contributions

MEB led study design and led writing of the manuscript, PJG co-led study design, led model training, tuning, and projections, and contributed to writing the manuscript, NTA, TM, HMT and ZL provided input data and contributed to model tuning decisions and writing the manuscript, and MDL, NH, EJS, and MX contributed to study design and writing the manuscript.

Data Accessibility

All model input data unique to this study and a full R markdown file of model tuning procedures with final results are included as online supplementary materials to this manuscript. Environmental input data used in this study are available for free online at worldclim.org (bioclim layers; Fick and Hijmans 2017) and at https://www.fos.auckland.ac.nz/our_research/karst/ (World Map of Carbonate Rock Outcrops v3.0; Ford and Williams 2007).

Supplementary Material

The following materials are available as part of the online article at <https://escholarship.org/uc/fb>

Appendix S1. FrancoisModelingSupplement.html: Rmarkdown file showing all steps for data processing and model tuning, model comparisons and calculation of metrics.

Appendix S2. SupplementalTablesFigures.docx: A document including all supplemental tables and figures cited in the manuscript.

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