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TITLE: Evaluating the Effectiveness of Conservation Site Networks under Climate Change: Accounting for Uncertainty.

RUNNING TITLE: Uncertainty in Impacts of Climate Change

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Abstract

We forecasted potential impacts of climate change on the ability of a network of key sites for bird conservation (Important Bird Areas; IBAs) to provide suitable climate for 370 bird species of current conservation concern in two Asian biodiversity hotspots: the Eastern Himalaya and Lower Mekong. Comparable studies have largely not accounted for uncertainty, which may lead to inappropriate conclusions. We quantified the contribution of four sources of variation (choice of general circulation models, emission scenarios and species distribution modelling methods and variation in species distribution data) to uncertainty in forecasts and tested if our projections were robust to these uncertainties. Declines in the availability of suitable climate within the IBA network by 2100 were forecast as “extremely likely” for 45% of species, while increases were projected for only 2%. Thus, we predict almost 24 times as many “losers” as “winners”. However, for no species was suitable climate “extremely likely” to be completely lost from the network. Considerable turnover (median = 43%, 95% CI = 35-69%) in species compositions of most IBAs were projected by 2100. Climatic conditions in 47% of IBAs were projected as “extremely likely” to become suitable for fewer priority species. However, no IBA was forecast to become suitable for more species. Variation among General Circulation Models and Species Distribution Models contributed most to uncertainty among forecasts. This uncertainty precluded firm conclusions for 53% of species and IBAs because 95% confidence intervals included projections of no change. Considering this uncertainty, however, allows robust recommendations concerning the remaining species and IBAs. Overall, while the IBA network will continue to sustain bird conservation, climate change will modify which species each site will be suitable for. Thus, adaptive management of the network, including modified site conservation strategies and facilitating species’ movement among sites, is critical to ensure effective future conservation.

Introduction

Identifying and safeguarding areas of suitable habitat to protect species of conservation concern from land-use change, hunting and other threats is central to conservation management (Hambler, 2004). Networks of such sites, representing a large range of climate and habitat types distributed over large geographical areas (hereafter conservation site networks), are considered vital to protecting biodiversity (Chape *et al.*, 2005; Butchart *et al.*, 2012). However, growing awareness that global climate change threatens biodiversity (Pereira *et al.*, 2010; Bellard *et al.*, 2012) has encouraged several assessments of the future viability of current conservation site networks given projected changes (Araujo *et al.*, 2004; Hannah *et al.*, 2007; Hole *et al.*, 2009; Araujo *et al.*, 2011). Generally, such networks have been established on the basis of recent or contemporary species' distributions (Gaston *et al.*, 2006; Hannah *et al.*, 2007). However, shifts in species' distributions due to climate change could mean that areas currently important for conservation priority species may not retain such species in the future (Araujo *et al.*, 2004; Hannah *et al.*, 2007; Hole *et al.*, 2009; Araujo *et al.*, 2011). Indeed, recent research on one European conservation site network suggests that future climates within a random set of sites could be as suitable for priority species as sites within the network (Araujo *et al.*, 2011). However, other networks, in Europe (Araujo *et al.*, 2011) and Africa (Hole *et al.*, 2009), are projected largely to maintain their effectiveness. Conservation site networks designed with both current and future species' distributions in mind may be more cost effective than adding new areas once the impact of climate change becomes apparent (Hannah *et al.*, 2007). Thus, explicit consideration of future species' distributions given climate change, and the consequences for area-based conservation is of increasing policy and planning relevance.

Progress towards considering species' future distributions in conservation decisions has been advanced by statistical tools that model species' distributions as a function of environmental covariates like climate (Elith *et al.*, 2006; Elith & Leathwick, 2009; Franklin, 2009; Thuiller *et al.*, 2009). When combined with General Circulation Model (GCM) projections of future climates, such species' distribution models (SDMs) can provide useful forecasts of where suitable climates for species might occur in the future. SDMs have been used to predict recent range shifts and population changes successfully (Hill *et al.*, 1999; Araujo *et al.*, 2005; Gregory *et al.*, 2009) and if carefully employed could contribute to conservation policy that is effective both now and in the future. These tools have stimulated an extensive literature assessing future biodiversity patterns given climate change (e.g.

Thomas *et al.*, 2004; Jetz *et al.*, 2007) and proposing adaptations to conservation policy (Carroll *et al.*, 2010; Hole *et al.*, 2011).

While SDMs have advanced our ability to plan for the future considerably, forecasting species' future ranges remains a major challenge (Davis *et al.*, 1998; Pearson & Dawson, 2003; Dormann, 2007b; Beale *et al.*, 2008). Using species' distribution models to identify conservation priority areas or adapt management strategies requires caution. One approach to making robust conservation recommendations is to consider the uncertainty surrounding projections of future climate and species' distributions (Elith *et al.*, 2002). This permits conservation policy to be informed by confidence in model results (Moilanen *et al.*, 2006). For example, if multiple modelling methods unanimously suggest a particular site will enhance a conservation network, this site should be prioritised over others for which support varies among methods. Uncertainty in projections may arise from several sources, including: errors in the source data, uncertainty in GCM projections, uncertainty in future emissions trajectories and choice of modelling methodology. Some authors have considered the importance of different sources of error explicitly (e.g. Dormann *et al.*, 2008; Diniz-Filho *et al.*, 2009; Buisson *et al.*, 2010; Garcia *et al.*, 2012), and several studies have combined multiple SDM approaches (ensemble methods, Araujo & New, 2007; Thuiller *et al.*, 2009; Araujo *et al.*, 2011). However, many studies of climate change impacts on species' distributions do not explicitly quantify the uncertainty among projections when making conclusions about specific species and areas, and often present averaged projections when multiple approaches are used (Elith & Leathwick, 2009). Averaging models with different underlying assumptions should improve estimates of changes in species distributions, and constitutes an important first step. However, in such situations it is still unclear how robust conclusions might be to uncertainties about future climate and the relationship between climate and species' distributions. For example, if the average projection for a species suggests decreased representation, but a few approaches forecast increases, this would indicate sensitivity to modelling assumptions, necessitating cautious interpretation. Even analyses that quantify model uncertainty do not investigate the consequences of this uncertainty for estimated impacts of climate change on conservation networks or identify the sources of uncertainty in this context.

Here, we focus on BirdLife International's Important Bird Area (IBA) network in two regions of Asia, the Eastern Himalayas and the Lower Mekong. IBAs form a global network of over 10,000 sites critical for avian conservation (BirdLife International, 2008), although half are currently not formally protected (Butchart *et al.*, 2012). IBAs are identified using standardised criteria relating to populations of (i) globally threatened; (ii) restricted-range; (iii) biome-restricted; or (iv) congregatory species. The focus of these criteria on species of conservation concern makes IBAs a useful system for evaluating climate change effects on conservation site networks. The IBA network in the biodiversity hotspots of the Eastern Himalaya (163 sites) and the Lower Mekong (140 sites, see Figure S1) are of particular interest because they support unique avifaunas in regions experiencing particularly rapid development and population growth, as well as substantial climate change (Christensen *et al.*, 2007), and because the impacts of climate change on these sites have not been evaluated.

We forecasted the ability of the IBA network to continue representing suitable climate for 370 bird species of conservation concern given projected climate change. We then assessed how robust conclusions based upon these forecasts were to uncertainty inherent in projecting models into the future. We quantified four sources of error in our forecasts including variation among: (i) GCMs, (ii) emission scenarios, (iii) SDM methodologies and (iv) data used to fit the SDMs. As variation within the data is probably spatially dependent we developed a novel method that accounts for spatial auto-correlation. We use the forecasted climate suitability of IBAs for each species and their associated uncertainties to address the following three questions: 1) how will projected climate change affect the representation of suitable climate for each priority species within the IBA network?, 2) how will climate change alter species richness and composition in each IBA?, and 3) which sources of error contribute most to uncertainty in the forecasts?

Materials and Methods

Species' distribution and IBA data

We obtained breeding distribution maps for 400 bird species of conservation concern (i.e. those listed as Threatened or Near Threatened on the IUCN Red List, plus restricted-range and biome-restricted species as defined by BirdLife International) as GIS shapefiles compiled by BirdLife International and NatureServe (2011, see http://www.birdlife.org/datazone/info/spcdownload). Taxonomy follows BirdLife International (2011, see http://www.birdlife.info/im/species/checklist.zip). We overlaid the breeding ranges of all species with a 30′ latitude x longitude grid (roughly 55 x 55 km at the equator) covering Asia (grey area in Figure S1), and considered species to be present in all cells they intersected. Species whose breeding ranges intersected <5 cells (22 species) were not considered further. By only considering species that currently breed in the focal regions, we may overlook some potential future colonists that originate beyond the region, which could alter projections of change in IBA species composition. However, our focus was on continued protection of species of conservation concern that currently occur within the region. Exploring potential colonists (or potential for assisted migration, Kostyack *et al.*, 2011) from species originating beyond the region is beyond the scope of this work. BirdLife International also provided GIS shapefiles for the boundaries of the 303 IBAs in the focal regions (coloured red in Figure S1).

Climate Data

Contemporary Climatic Data

Mean monthly temperature, precipitation and percentage sunshine data for 1951-2000 (a period corresponding to the majority of data underlying the species' range extent maps) were obtained from Worldclim (Hijmans *et al.*, 2005, http://www.worldclim.org/) and CRU-TS2.1 (Mitchell & Jones, 2005, http://www.ipcc-data.org/obs/cru_ts2_1.html). Soil water capacity data were obtained from Prentice *et al.* (1992). These data were used to calculate four bioclimatic variables previously found useful when modelling bird distributions (Huntley *et al.*, 2006; Hole *et al.*, 2009; Araujo *et al.*, 2011) at a 30□ resolution. These variables, chosen *a priori,* were mean temperatures of the coldest and warmest months, the ratio of actual to potential evapotranspiration and the seasonality of moisture availability. The methods used to calculate these bioclimatic variables are described in detail in the Supporting Information.

Future Climate Projections

We forecast species' distributions for three time periods (2011-40, 2041-70 and 2071-2100, henceforth referred to as 2025, 2055, 2085 respectively) using projections of future climate under three emissions scenarios (IPCC Special Report Emissions Scenarios; SRES) and four GCMs. The three SRESs (A2, A1B and B1) were developed by the IPCC Special Report on Emission Scenarios (IPCC, 2000) to represent the plausible range of demographic, economic and technological drivers that may affect future emissions. The increase in global temperature by the end of the 21st century is projected to be greatest under the A2 scenario (3.1^{o}C), followed by the A1B scenario (2.7^{o}C) and least under the B1 scenario (1.8^{o}C) (Meehl *et al.*, 2007). The four GCMs (HadCM3, MPI-ECHAM5, GFDL-2.1 and NCAR-CCSM3) were selected to represent the range in projected climates presented in the IPCC Fourth Assessment Report (AR4, IPCC, 2007). Projections of future precipitation patterns range considerably among GCMs and these models represent this variation. Projections from HadCM3 and GFDL-2.1 are drier than the ensemble mean presented by the IPCC AR4 (Meehl *et al.*, 2007) while NCAR-CCSM3 and MPI-ECHAM5 are wetter than the mean.

Extracting present and future climates for the IBAs

We calculated bioclimates for individual IBAs to account for their large variability in extent and consequently in climatic representation. Present climate data were obtained at, or interpolated to (see Supporting Information), a 2.5□ resolution (c. 4.6 x 4.6 km at the equator). Projections of future climate were obtained for the 36 combinations of three time periods, four GCMs and three SRESs from the World Data Center for Climate, Hamburg, Germany (http://cera-www.dkrz.de). We calculated anomalies between the projected 1951–2000 climates from each GCM and their respective projections of future climates under each SRES scenario. These anomalies were applied to the observed 1951–2000 climate data to develop projections of future climates (see Supporting Information). These projections were downscaled from the original GCM resolution to a 2.5□ resolution using the change-factor approach (Wilby *et al.*, 2004; Tabor & Williams, 2010; see Supporting Information). We overlaid these fine scale grids with the boundaries of each IBA and extracted data from all intersecting cells. We also recorded the proportion of each 2.5□cell that lay within the IBA. These climate data were used to calculate the four bioclimatic variables described above for the present and future for every cell in each IBA.

The projected future bioclimates included some values for individual bioclimatic variables that do not currently occur in Asia. Projecting species' distributions under such bioclimates involves extrapolating beyond the range of data used in fitting the SDMs, which can be misleading (Fitzpatrick & Hargrove, 2009). Therefore, we set any bioclimatic variables that were outside the observed range to their closest value in the 1951-2000 period (i.e. the maximum or minimum observed value), a procedure known as "clamping" (Phillips *et al.*, 2006). A small proportion of the total area of IBAs required clamping for the time period centred on 2025 (median across GCMs and SRES scenarios of 1% of total IBA area) , increasing to 4% in 2055 and 14% in 2085 (Figures S2 and S3).

Species' distribution models

We employed four widely-used modelling techniques to estimate how climate influences species' distributions: Generalised Linear Models (GLMs, McCullagh & Nelder, 1989), Generalised Additive Models (GAMs, Hastie & Tibshirani, 1990; Wood, 2006), Boosted Regression Trees (BRTs, Ridgeway, 2006; Elith *et al.*, 2008) and Random Forests (RFs, Breiman, 2001; Cutler *et al.*, 2007). These methods were chosen because they perform well in comparisons of techniques (Araujo *et al.*, 2005; Prasad *et al.*, 2006; Meynard & Quinn, 2007; Elith & Graham, 2009; Franklin, 2009; Wenger & Olden, 2012) and provide a contrast between semi-parametric (GLMs and GAMs) and machine-learning approaches (BRTs and RFs).

Dealing with spatial dependence

A concern with many species distribution modelling techniques (including those used here) is a failure to account for spatial autocorrelation (Dormann, 2007a; Dormann *et al.*, 2007; Beale *et al.*, 2008; Beale *et al.*, 2010). To deal with this problem we estimated the transferability of the fitted models to spatially segregated test data (*k*-fold partitioning) and then used a non-parametric jack-knife to estimate the uncertainty in model predictions. The data were split into sampling units defined on the basis of Asian ecoregions (Olson *et al.*, 2001 http://www.worldwildlife.org/science/data). The same ecoregion often occurs in several, geographically distinct locations; non-contiguous areas of an ecoregion were considered separate sampling units. A few very large ecoregions (greater than 450,000 km^2 in area, roughly 6^o x 6^o) were split into smaller sampling units by intersecting them with a 6^o x 6^o grid and treating parts of the ecoregion in different grid squares as separate sampling units. This ensured that subsequent blocks formed by grouping the sampling units were similar in size. We grouped sampling units into 10 blocks so that the mean of the bioclimatic variables differed little among blocks but each block spanned the full range of bioclimates (using the '*blockTools'* package in *R*). This ensured that block and bioclimate were orthogonal and avoided truncation of species response curves, which can cause problems when analysing segregated data (Thuiller *et al.*, 2004).

We left out each block in turn (to be used as test data) and fitted our models to the remaining (training) data. We evaluated model performance, using the Area Under the Curve of the receiver-operating characteristic plot (AUC , Hanley & McNeil, 1982), by assessing ability to predict the distribution of the species within the test block. Variation among the 10 models provided a measure of the uncertainty in estimates of climatic suitability for each species. This approach ensured that the test data were spatially segregated from the training data (unlike standard *k*-fold partitioning where data are divided at random) while the range of the predictors was similar in the training and testing data (unlike when data are separated into geographic regions). More complex modelling methods often fail to perform well when analysing data from large regions (Beale *et al.*, 2010), possibly because of non-stationarity in the scale and direction of spatial dependence and the strong spatial auto-correlation in climatic data. Our non-parametric approach was flexible enough to capture this complexity.

Generalised Linear Models

We used generalised linear models (McCullagh & Nelder, 1989) to fit polynomial relationships between each species' occurrence (at a 30 grid cell resolution) and bioclimate. We used cross-validation to determine the degree of the polynomial relationship between bioclimate and species occurrence, up to a maximum degree of four. For each species, we excluded one block at a time and fitted 256 models of species occurrence as a function of the four bioclimatic variables. The models included each possible combination of polynomial degree (1 – 4) for the four bioclimatic variables (4 variables^4 polynomial degrees = 256 combinations). Model ability to predict species occurrence in the excluded block was assessed using AUC. The combination of polynomial degrees that maximised the average AUC across the 10 omitted blocks was used to fit a final set of 10 models; one omitting each block in turn. The median AUC across these models provided a measure of the models' fit and transferability.

Generalised Additive Models

Non-linear relationships between species' occurrence and bioclimate were fitted as thin-plate regression splines with the smoothness established using generalised cross-validation (Wood, 2006). The presence or absence of each species in each 30□ grid cell was modelled as a Bernoulli response, using a logit link. These models were fitted to each species' data excluding a block at a time using the '`gam()`' function from the '*mgcv'* package in *R* (R Development Core Team, 2011). The median AUC (calculated using the omitted block) from the 10 models was used to evaluate the models' fit and transferability.

Boosted Regression Trees

Boosted Regression trees (BRT) use machine learning to establish the (potentially non-linear) relationship between predictors and response (Friedman, 2002; Ridgeway, 2006; Elith *et al.*, 2008). Modelling with BRTs involves setting three important parameters: the learning rate (*lr*), which controls the weight that is given to each component tree; the tree complexity (*tc*), which controls the number of nodes within each tree; and the number of trees (*nt*) kept in the final model. Optimising these parameters maximizes accuracy and transferability. We used the following cross-validation approach to select these parameters for each species. We excluded one block from the data at a time and fitted a BRT with 15,000 trees using three values of *lr* (0.01, 0.005 and 0.001) and four values of *tc* (1 – 4). For each combination of *lr* and *tc*, we identified the *nt* (1 – 15,000) that best predicted data from the omitted block. Any combinations requiring <1000 or >10,000 trees were excluded. Models are recommended to have >1000 trees to minimise the influence of any single component tree (Ridgeway, 2006; Elith *et al.*, 2008) and models with >10,000 trees may require more trees than attempted to converge. The set of parameters (*lr, t*c and *nt*) that returned the minimum summed error across all the blocks was used to fit a final set of 10 BRT models; each model fitted to data excluding one block in turn. The median AUC provided a measure of model fit and transferability.

Random Forests

Random Forests is a machine learning approach that builds regression and classification trees to describe the relationship between the response and predictors (Breiman, 2001; Prasad *et al.*, 2006; Cutler *et al.*, 2007). Multiple trees are built, each based on a bootstrap sample of the data and a random subset of the predictors. The final model predictions are an average prediction across component trees. Random forests require two main parameters to be chosen the number of trees: (*nt*) and the number of predictors used to build each tree (*m)* (Prasad et al., 2006). We used cross-validation to optimise these two parameters. The number of predictors, *m*, was set to 1 – 3 and a random forest with 1000 trees was fitted omitting each block in turn. The ability of the model to predict the species' occurrence in the omitted block was assessed using AUC. A further 500 trees were then added and the AUC for the omitted block computed again. If the larger model improved the AUC by more than 1% it was accepted. This was repeated iteratively until additional trees did not improve the AUC further. The value of *m* that maximised mean AUC for the excluded data across the 10 blocks and the maximum *nt* used across the blocks was used to fit final models for the species, excluding each block in turn. The median AUC of these models when predicting data from the excluded block was used to measure model fit and transferability.

Predicting the future effectiveness of the IBA network

Estimating climate suitability within each IBA

The 40 models (10 jack-knife iterations x 4 SDMs) were used to predict the probability that each IBA might contain suitable climate for each species using present climate and the 36 future climate projections. We used the bioclimatic variables from each 2.5□ climate cell (*i*), in each IBA (*j),* to calculate the probability that each species *(k)* might find suitable climate within that cell in time-period *t* ($p_{ijk}[t]$). The SDMs were fitted to species occurrence data at 30□ resolution and because larger cells are more likely to contain suitable climate than smaller ones, this has to be corrected for when projecting to different sized cells (Alagador *et al.*, 2011). Therefore, the probabilities were adjusted to account for the smaller size of the 2.5□ cells by using the following relationship (based on a binomial distribution).

$$\hat{p}_{ijk}[t] = 1 - \left(1 - p_{ijk}[t]\right)^{A_{ij}/0.5^2} \qquad \text{(eq. 1)}$$

where A_{ij} is the area of cell *i* (in degrees) that lies within IBA *j*. An IBA may cover several 2.5□ cells, so an aggregate estimate of whether species *k* would find suitable climate somewhere within IBA *j*, with *n* cells, was calculated as

$$P_{jk}[t] = 1 - \prod_{i=1}^{n}\left(1 - \hat{p}_{ijk}[t]\right) \qquad \text{(eq. 2)}$$

The difference in $P_{jk}[t]$ between the present and a future projection is a measure of the change in climate suitability within IBA *j* ($\Delta P_{jk}[t]$) for species *k*. The projected species richness within an IBA can be estimated by summing the probabilities that each of the *s* species modelled would find suitable climate within each IBA. Thus, the species richness within IBA *j* is estimated as

$$S_j[t] = \sum_{k=1}^{s} P_{jk}[t] \qquad \text{(eq. 3)}$$

Subtracting predicted present species richness for an IBA from $S_j[t]$ gives an index of the projected change in species richness $\Delta S_j[t]$. To estimate projected turnover, $T_j[t]$, of species between the present and future projection for time-period *t*, we used the Bray-Curtis index that measures dissimilarity between two communities (Bray & Curtis, 1957) and is a continuous analogue of the turnover metric used in previous papers (e.g. Hole *et al.*, 2009)

$$T_j[t] = \frac{\sum_{k=1}^{n}\left|P_{jk}[t]-P_{jk}[0]\right|}{\sum_{k=1}^{n}P_{jk}[0]+\sum_{k=1}^{n}P_{jk}[t]} \qquad \text{(eq.4)}$$

To test the ability of our models to predict the suitability of each IBA in the network for the study species, we obtained species inventories from 130 IBAs located in four focal countries (Cambodia, Laos, Nepal and Vietnam). We compared the inventory of each IBA to the models' projections of present climate suitability for each species within the IBA (i.e. $P_{jk}[present]$). We calculated the AUC for this comparison to quantify the performance of the models.

Summaries for individual species

To evaluate how climate change might affect an individual species, *k*, across the entire network, we summed $P_{jk}[t]$ across all the IBAs. This provides an estimate of how many IBAs are projected to contain suitable climate for species *k*. Subtracting the estimate of P_{jk}[t] for the present from each future climate simulation provides an index of the overall change predicted for species *k* under climate change, $\Delta P_k[t]$.

Quantifying forecast uncertainty

Using every combination of jack-knife iteration, SDM, GCM, and SRES scenario (480 predictions) we calculated $\Delta S_j[t]$ and $T_j[t]$ for every IBA and $\Delta P_k[t]$ for each species between the present and each of the three future time periods. We calculated the median values across these projections for each species or IBA. To quantify the uncertainty in these estimates we calculated the 95% quantiles of the distribution of values across the 480 projections. We refer to changes where these quantiles do not overlap 0 as 'extremely likely', following the terminology of the IPCC 4th Assessment Report (IPCC, 2007, pp. 22-23). We do not refer to these changes as 'significant' because the choices of SDM, GCM and SRES scenario were not made at random, but reflect considered choices from several discrete options. Throughout the text we present the results for the time-period centred on 2085, along with maps when relevant.

Identifying the sources of uncertainty

We quantified variation in the end-of-century projections of $\Delta P_k[2085]$, $\Delta S_j[2085]$ and $T_j[2085]$ due to SRES scenario, GCM, SDM and jack-knife iteration using variance component analysis. $T_j[t]$ was logit-transformed prior to analysis to satisfy the assumption of normality (Warton & Hui, 2011). Species or IBA were also included in the models. We calculated both the variance component due to the main effect of each source of variation and its interaction with species or IBA. The main effects provide information on the impact of different components of uncertainty on the overall conclusions (i.e. average loss of suitable climate across all species or average species richness change or average turnover across all IBAs). The interactions provide information about the contributions of components to projections for individual species or IBAs.

Results

Model evaluation

Models were fitted successfully to 370 species. Of the initial 400 species, 13 did not breed in the focal regions, nine occurred in < 5 grid cells, three were restricted to a single block, and one of the four modelling methods failed to converge for five species. Model fit was very good for most species. The median AUC across the 10 models fitted to each species' present distribution ranged between 0.862-0.999 (median = 0.990) for the GLMs, 0.873-0.999 (median = 0.989) for the GAMs, 0.854-0.999 (median= 0.990) for the BRTs and 0.620-0.999 (median = 0.991) for the Random Forests. The models also performed well when projecting present assemblages within the 130 IBAs for which inventories were available (median AUCs: GLMs=0.857; GAMs = 0.862; BRTs = 0.873, Random Forests = 0.882). AUC values >0.9 reflect very good discrimination and those >0.7, useful discrimination (Swets, 1988; Franklin, 2009).

Impacts on individual species

The models projected that by the end of the 21st century (2085) the vast majority of the 370 species analysed (88%) will experience reduced availability of suitable climate within the IBA network (i.e. median $\Delta P_k[2085] < 0$ across GCMs, SRES scenarios, SDMs and jack-knife iterations; Figure 1). Suitable climate for each species was projected to disappear from about 4 IBAs on average by 2085, but there was substantial variation among species (median $\Delta P_k[2085] = -4.1$ IBAs, 95% CI across species = -14.8 – 3.0 IBAs). This equates to, on average, suitable climate for species being lost from about 29% of the IBAs that are currently climatically suitable. There was also substantial variation among projections for each species among SRES scenarios, GCMs, SDMs and jack-knife iterations. After accounting for this uncertainty, 45% of species were projected as ‘extremely likely’ to decline (i.e. the upper 97.5% of ΔP_k from all combinations of SRES scenario, GCM, SDM and jack-knife iterations were <0; filled portion of bars in Figure 1). Over the same period, around 2% of species were projected as ‘extremely likely’ to find more suitable climate within the network. Overall, the models projected approximately 24 times as many “losers” as “winners” among these species of conservation concern. However, complete loss of suitable climate from the IBA network by 2085 was not “extremely likely” for any species considered (i.e. the probability of finding at least some suitable climate within the network was >5% for all species).

Accounting for variation among projections alters our interpretation of the results, sometimes considerably. For example, the median projection for 51 species suggested that they would be found in 10 fewer IBAs by 2085 (median $\Delta P_k[2085] < -10$). However, the 97.5% quantile of the projections for 49 of these species suggested they would be lost from fewer IBAs. Thus, the analyses only support such dramatic losses of representation in IBAs for the remaining two species (*Hypsipetes leucocephalus* and *Pericrocotus brevirostris*).

Impacts on IBAs

By the end of the 21st century, 89% of IBAs were projected to become climatically suitable for fewer of the species considered. Once again, these projections were accompanied by considerable uncertainty due to variation among GCMs, SRES scenarios, SDMs and jack-knife iterations. After accounting for this uncertainty, 47% of IBAs were projected as ‘extremely likely’ to be suitable for fewer species by 2085 (Figure 2). In contrast, only 11% of IBAs were projected to become suitable for more species by 2085 and this was ‘extremely likely’ for *no* IBAs. The models projected a median loss of suitable climate for 2.8 species of conservation concern per IBA by 2085 (95% CI=-8.9 – 0.6 species per IBA) which corresponds to about 37% of such species that an IBA is currently climatically suitable for. Projected species richness loss was significantly greater for fully protected IBAs than for partially protected or unprotected IBAs (median species loss in protected IBAs was greater by 1.87 species, 95% CI = 3.78 – 0.43 species). However, the proportion of species lost was not significantly different between fully protected IBAs and partially or unprotected IBAs (median proportional species loss in protected IBAs was 3.9% lower, 95% CIs = -1.1 – 1.3%). Generally, IBAs in the Lower Mekong were affected more negatively by projected climate change than IBAs in the Eastern Himalaya. By 2085, 59% of IBAs in the Lower Mekong were projected as 'extremely likely' to lose suitable climate for species compared to 37% of IBAs in the Eastern Himalaya.

Overall, median turnover in species of conservation concern increased from 19% in 2025 (95% confidence range = 14 – 45%) to 43% in 2085 (35 – 69%, Figure 3). There was considerable variation among projections of turnover for the IBAs (Figure 3). There was little difference in species turnover between protected and unprotected IBAs (median turnover was 1.5% lower in protected IBAs, 95% CI = -6.8 – 2.6%). In contrast to the regional differences in species loss, median projected turnover was very similar in the two regions: 42% (22 – 70%) in the Eastern Himalaya and 44% (24 – 67%) in the Lower Mekong.

Taking variation among projections into account affected our inferences about changes in IBAs. For example, according to median projections, 60 IBAs (20%) were forecast to lose >10 species by the end of the century. However, this level of species loss was only supported for 13 IBAs (4%) once uncertainty among projections was accounted for (i.e.

the upper 95% limit for the remaining IBAs were >-10). Similarly, median turnover of >50% was projected for 99 IBAs (33%) by 2085. However, in all these cases, the lower 95% quantiles of the turnover projections were <50%, so such drastic turnover was not 'extremely likely' for any IBA.

Components of uncertainty

Choice of GCM, SRES scenario and SDM all contributed substantially to forecast uncertainty (Table 1). Variation among projections of future climates (GCMs and SRES scenarios together) was the biggest source of uncertainty for overall estimates of mean $\Delta P_k[2085]$, $\Delta S_j[2085]$and $T_j[2085]$. Variation among SRES scenarios had a larger impact on uncertainty in turnover than on uncertainty in changes in species representation or species richness. In fact, variation among SRES scenarios made the largest contribution to uncertainty in average IBA turnover, with the median projected turnover by 2085 under the A2 scenario about 12% higher than that under the B1 scenario (Figure 3). Choice of SDM technique also contributed substantially to variation in mean turnover across IBAs, with median turnover for the random forest projections approximately 9% higher than those for GLMs. The difference between projections from the machine learning and semi-parametric methods was very small (a comparison of models with and without a term for model type suggested no significant difference; $\chi^2_1=0.51$, $P=0.48$). Variation among SDM techniques was also important for projections for individual species and IBAs, as indicated by the relatively large amount of variation attributed to the interactions between SDM and species or IBA (10–14 %, Table 1). Indeed the species x SDM interaction was the largest source of variation in projections of change for individual species. GCMs also contributed considerably to variation among projections for individual species and IBAs, explaining the most variation for projections of species richness change and turnover for individual IBAs. Variation among jack-knife iterations contributed least to the overall uncertainty in forecasts for species and particularly for IBAs. While the contribution of jack-knife iteration was small, it was not necessarily unimportant (it explained >10% of the variation in forecasts for about 17% of species). However, in general, uncertainty arising from projections of future climate and modelling methods was much greater.

Discussion

The impact of recent climate change on species distributions (Thomas *et al.*, 2004; Chen *et al.*, 2011) makes evaluating its future consequences for the effectiveness of conservation programmes a priority (Araujo *et al.*, 2004; Hannah *et al.*, 2007; Hole *et al.*, 2011). While forecasting the fate of biological communities using models based on correlations will always be fraught with uncertainties, evaluating the performance of models and measuring the uncertainty associated with their predictions makes this process more robust (Elith *et al.*, 2002; Garcia *et al.*, 2012). These steps enable identification of deficiencies in methodology or data and often suggest improvements. It is standard for SDM applications to provide assessments of model performance (e.g. AUC, Cohen's Kappa), but information on the variation among predictions due to climate projections, modelling approach and variation in the training data is rarely provided. In this study, we explicitly quantified this variation, with important ramifications for our conclusions and potentially for resultant conservation management recommendations. Median projections for almost 90% of the species considered here suggested decreased representation within the IBA network by the end of the 21st century. However, in half of these species, the results depended on the methodology, making strong recommendations in these cases inadvisable. Nevertheless, almost half of the species and IBAs were projected as 'extremely likely' to be negatively impacted by climate change even after accounting for uncertainty surrounding projections.

Conversely very few species (2%) were ‘extremely likely’ to be more widespread in IBAs in the future and no IBAs were ‘extremely likely’ to protect more species. This supports the emerging consensus that climate change will affect the representation of species of conservation concern in conservation site networks (Hole *et al.*, 2009; Araujo *et al.*, 2011; Hole *et al.*, 2011) and suggests that this conclusion is independent of the methodology used to project species’ distributions.

The magnitude of climate change is projected to be relatively high in both the Eastern Himalaya and the Lower Mekong (Christensen *et al.*, 2007; Williams *et al.*, 2007). Greater seasonality of precipitation is predicted in south and south-east Asia, with intensification of both wet and dry seasons indicated by GCM projections (Christensen *et al.*, 2007). Thus, large and widespread impacts on bird communities are not unexpected. These results for the Asian IBA network are consistent with those for other regions of the world. Hole *et al.* (2009) projected that by 2100 African IBAs would experience a turnover among conservation priority species of 35-45% (compared to 43% for the Eastern Himalaya and Lower Mekong over the same period). Araujo *et al.* (2011) projected that 64% of Red-listed bird species currently found in Europe would lose representation in protected areas by 2080. We project a similar percentage of priority bird species as ‘extremely likely’ to lose representation in the Asian IBA network (45%). Because the methods used in these three studies have important differences (neither Hole *et al.* 2009 nor Araujo *et al.* 2011 quantify uncertainty explicitly), it would be unwise to make strong conclusions about the relative impacts of climate change on the three continents. Nonetheless, these studies agree that climate change could potentially drive substantial changes in the species composition of conservation areas globally.

Variation among projections of future climate (GCMs and SRES scenarios) was the biggest contributor to uncertainty in overall estimates of climate change impacts. The projections of future climates for both south and south-east Asia vary substantially between climate models (Christensen *et al.*, 2007). This is due to insufficient observational data for parts of both regions, an incomplete understanding of how changes in El Niño - Southern Oscillation (ENSO) might affect regional monsoon and tropical cyclone patterns, and the complex topography and coastal margins (Christensen *et al.*, 2007). Variability among SDM methodologies was also important, especially for projections for individual species (where it was the largest contributor) or IBAs. Other studies (Diniz-Filho *et al.*, 2009; Buisson *et al.*, 2010; Garcia *et al.*, 2012) have also highlighted variation among GCMs and SDM techniques as major contributors to uncertainty in projected species distributions. Overall however, in this study, the consequences of SDM methodology were more relevant for individual species than for overall conclusions about communities and regions, which were affected more by uncertainty in projections of future climate. This may be because differences among SDM techniques ‘average out’ when calculating aggregate measures of change (like species richness change or turnover) over multiple species. This could explain why SDM method contributed most to variation in projections for individual species (because the influence of GCMs and SRES scenarios were averaged across the 303 IBAs) while GCM contributed most to variation in projections for IBAs (because the influence of SDM techniques were averaged over the 370 species). While uncertainty in the data, including spatial dependency, contributed to overall projection uncertainty, its contribution was dwarfed by that from other sources. This may suggest that while the issue of spatial dependence is important for models of individual species’ distributions (Beale *et al.*, 2008), it may be less critical when the goal is to infer general effects of climate change on regions and communities.

There are several additional sources of uncertainty when projecting species' distributions into the future that we have not considered in this study. First, we made an *a priori* choice of climatic predictors of species distributions. It is likely that the distributions of some of the species included in this study are more constrained by other, unconsidered, climatic variables. Models based on different predictors may yield alternative projections of species' future distributions, adding a further layer of uncertainty. The models presented here ignore interactions among species that could potentially affect climate change impacts on species' distributions and community dynamics (Davis *et al.*, 1998; Suttle *et al.*, 2007). We also ignore the potential for species to acclimate or adapt to future climates as has been proposed elsewhere (Dawson, 2011). Our projections assume that species will be able to disperse from areas of present to future climatic suitability. Whilst some studies have demonstrated that species are capable of adjusting their ranges to match the changing distribution of suitable climate (Chen *et al.*, 2011), this is far from certain for all species, and several recent studies have highlighted species lagging behind changes in climate (Willis *et al.*, 2009; Devictor *et al.*, 2012). Finally, both the Lower Mekong and Eastern Himalaya are projected in part to have climates by 2100 that have no present-day analogues (Williams *et al.*, 2007). This adds an additional uncertainty to the analysis, because rather than extrapolate for such no-analogue climates we chose to 'clamp' predictor values to the range observed in the period 1951-2000. All these factors create further uncertainties in projections, but ones that are difficult to quantify. Developing methods that address these additional sources of uncertainty quantitatively and integrate them into analyses provides a future challenge for species' distribution modelling.

There is growing consensus that climate change will alter species' distributions and that this will have consequences for the future efficacy of conservation networks. In this study, we provide evidence that this conclusion is robust to many of the uncertainties in future climate change projections and species' distribution models. Evidence that climate change will influence the effectiveness of conservation networks is only the first step in informing more robust conservation strategies. The high turnover in the avifauna of the IBAs considered here suggests that facilitating movement of species among IBAs in the network may be important for its continued effectiveness. One important step to adapting conservation networks for climate change therefore is identifying and conserving contiguous areas of habitat through which species will be able to move between sites that are suitable now and sites suitable in the future. Sites projected to contain climates suitable for priority species in the future may also have to be added to the network. Recent progress has been made towards achieving these goals (Phillips *et al.*, 2008; Carroll *et al.*, 2010; Hole *et al.*, 2011) and this has been facilitated by the increasing availability of analysis tools both for understanding climatic constraints on species' distributions (Elith *et al.*, 2006; Elith & Leathwick, 2009; Franklin, 2009) and for conservation site network design (Moilanen *et al.*, 2006; Phillips *et al.*, 2008; Ball *et al.*, 2009; Fuller *et al.*, 2010). In addition, because it is only feasible for a small portion of the landscape to be protected formally, management options that maximise the permeability of surrounding landscapes (e.g. production forests and agricultural land) to wildlife populations should be considered (Kostyack *et al.*, 2011). Some species may not be able to move between current and future areas with suitable climate, indicating that translocation (or even *ex situ* conservation) may need to be considered (Araujo *et al.*, 2004; Hoegh-Guldberg *et al.*, 2008; Kostyack *et al.*, 2011). It must be acknowledged that sometimes managing individual sites for particular species or assemblages may be rendered futile by climate change (Hole *et al.*, 2009), so occasionally, resources may be better spent on other sites or adapting management to facilitate successful establishment of other species (Fuller *et al.*, 2010; Jackson & Sax, 2010; Hole *et al.*, 2011).

This study highlights that while there is considerable uncertainty associated with projecting the impacts of climate change on conservation site networks, robust conclusions are still possible when these uncertainties are accounted for. In particular, our analyses suggest that while climate change will substantially alter the distribution of suitable climate for many species, the existing conservation site network has potential to continue protecting species of conservation concern. Adapting management plans to cope with a changing climate will involve considerable effort, both in developing management plans and evaluating their effectiveness. Monitoring such management plans will be more informative if the uncertainties are considered explicitly. This should lead to conservation policy that is more robust to an uncertain future.

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Table 1: The components of uncertainty in projections of change by 2085 in the number of suitable IBAs for each species ($\Delta P_k[2085]$) and change in species richness ($\Delta S_j[2085]$) and turnover in species composition for each IBA ($T_j[2085]$). The percentage variance in projections for each species or IBA due to Emissions Scenario (SRES), General Circulation

Model (GCM), modelling methodology (SDM) and data variation, including spatial autocorrelation (SIM), were estimated using variance components analysis. The main effect for each component indicates its contribution to uncertainty in the mean projection across all species or IBAs; the interactions represent their contribution to uncertainty in projections for individual species or IBAs.

Change in species representation ΔP_k[2085]		**Change in IBA species richness ΔS_j[2085]**		**Turnover in IBA species composition T_j[2085]**	
Source	**% Variance**	**Source**	**% Variance**	**Source**	**% Variance**
Species	59.81	IBA	47.05	IBA	44.40
SRES	1.35	SRES	0.94	SRES	9.07
GCM	2.82	GCM	1.91	GCM	0.94
SDM	0.84	SDM	0.58	SDM	3.28
SIM	0.09	SIM	0.07	SIM	0.09
Species x SRES	2.18	IBA x SRES	2.17	IBA x SRES	0.97
Species x GCM	10.62	IBA x GCM	27.45	IBA x GCM	19.01
Species x SDM	14.12	IBA x SDM	9.94	IBA x SDM	11.90
Species x SIM	1.24	IBA x SIM	0.50	IBA x SIM	0.76
Residual	6.93	Residual	9.39	Residual	9.58

Figure Legends

Figure 1: Projected impacts of climate change on the representation of suitable climate for 370 species of conservation concern within the IBA network in the Eastern Himalaya (163 sites) and the Lower Mekong (140 sites). The histograms show the distribution of median changes in representation of species within the network. The height of each bar is the number of species projected with a median change in representation (in terms of number of IBAs) indicated on the x-axis. The filled portion of each bar is the number of species that are 'extremely likely' to show the direction of change indicated. Open portions of the bars indicate the number of species where the direction of change was not consistent across projections from combinations of SDM methodology, jack-knife iteration and GCM (the 95% quantiles overlap 0). The panels represent combinations of 30-year time-period (rows) and SRES scenario (columns).

Figure 2: Projected impacts of climate change on species richness in 163 IBAs in the Eastern Himalaya (top left) and 140 IBAs in the Lower Mekong (bottom left). The maps show projected changes in the number of species of conservation concern for which there is suitable climate in each IBA between the present and the end of the 21st Century. Future climates in coloured IBAs are "extremely likely" to be suitable for fewer species (red) or more species (blue). Colour intensity indicates the magnitude of the projected change. IBAs where there is no consistent trend (95% quantiles overlap 0) among the projections using different SRES scenarios, GCMs, SDM methods and jack-knife iterations are filled with grey. The histograms show the distribution of changes in species richness for the IBAs across combinations of 30-year time-periods (rows) and SRES scenarios (columns). The height of each bar represents the number of IBAs projected to experience a change of magnitude indicated on the x-axis. The filled portion of each bar indicates the number of IBAs that are 'extremely likely' to experience a change of that magnitude (the colour of the bar matches the

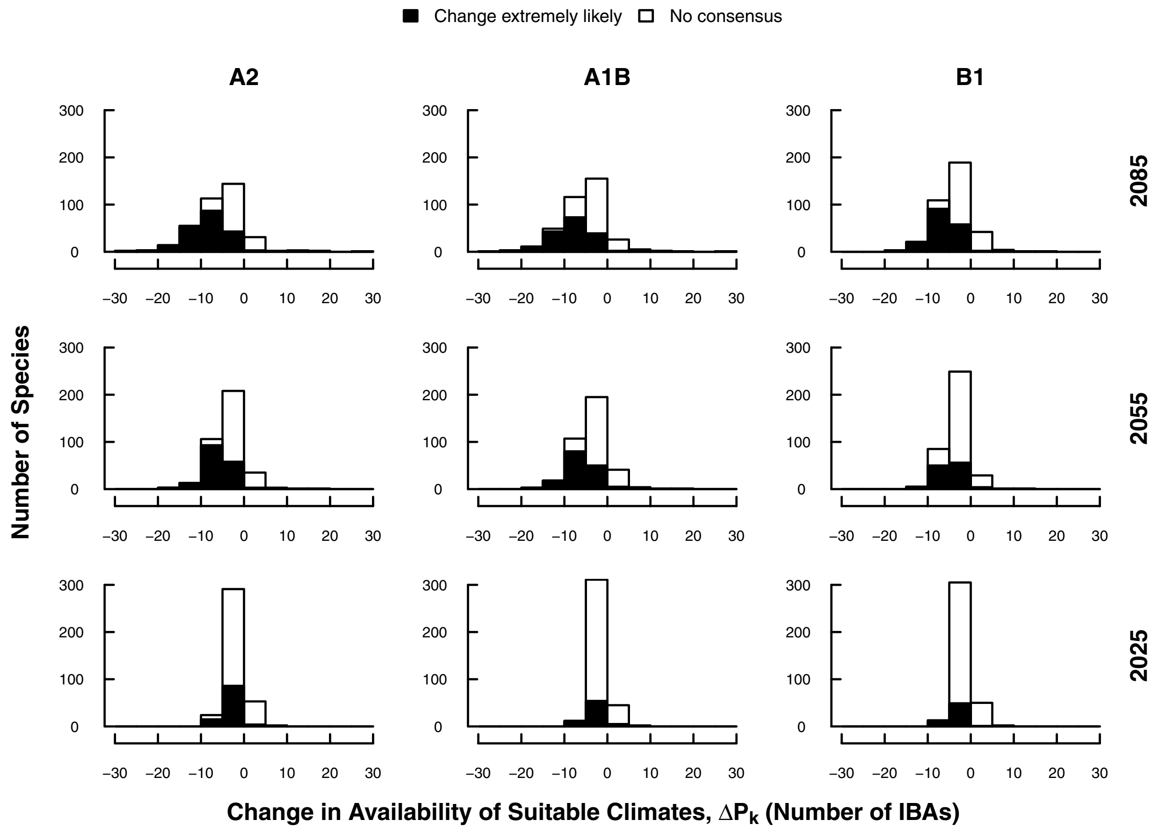
colours in the maps). The grey portion indicates the number of IBAs lacking no consensus across projections.

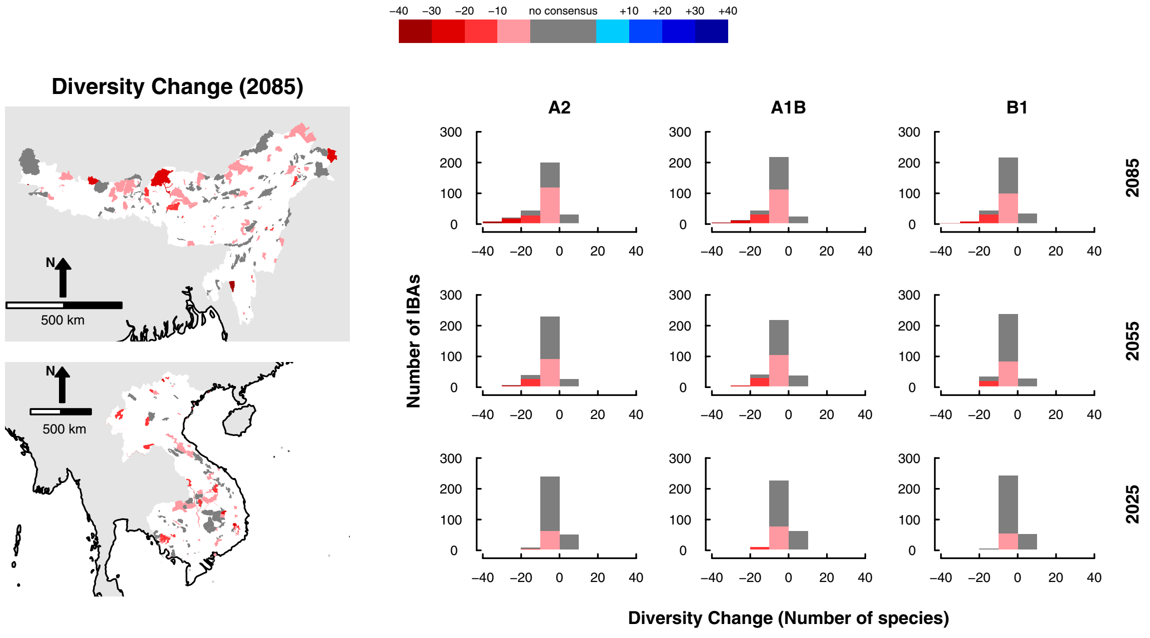
Figure 3: Projected percentage turnover in species composition within 163 IBAs in the Eastern Himalaya (top left) and 140 IBAs in the Lower Mekong (bottom left) by the end of the 21st Century. The colour of each IBA polygon indicates the projected turnover in species composition. The plots show the projected turnover in combinations of three 30-year time-period (rows) and three SRES scenarios (columns). The solid lines show the number of IBAs with a median projected turnover less than the value on the x-axis. The region shaded in grey represents the area where 95% of the projections lie (across the SDM methodologies, jack-knife iterations and GCMS). The colour bars displayed at the bottom of each plots match the colours in the maps. The vertical dashed lines indicate the median turnover for each SRES scenario x time-period combination.

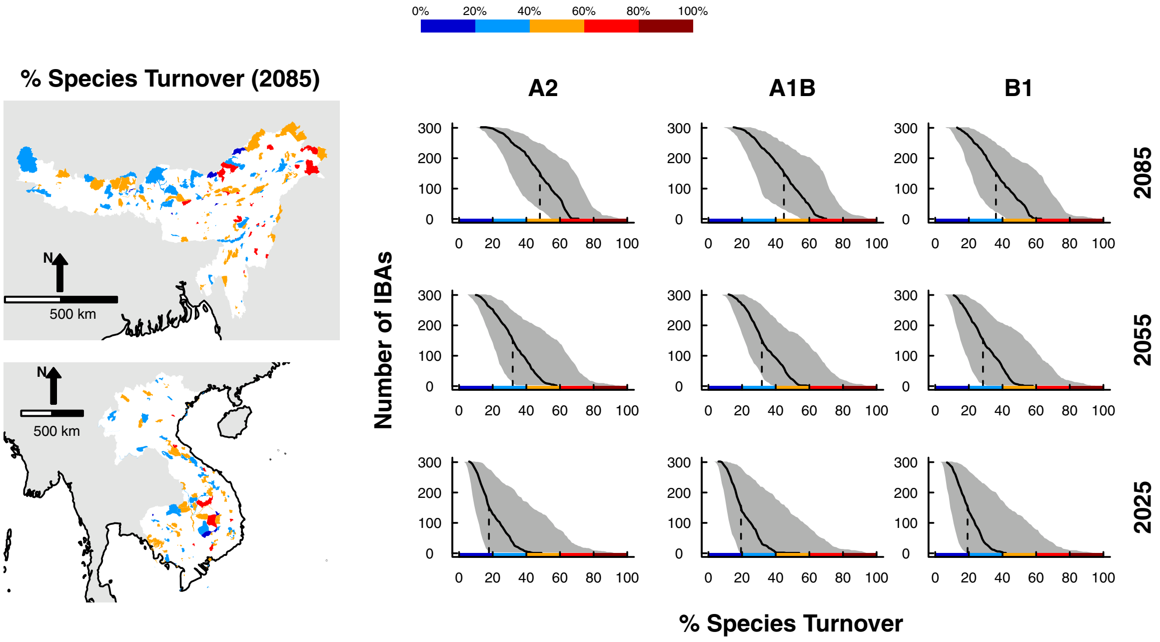
Figure S1: Map of Asia with the two study regions, the Eastern Himalayas and Lower Mekong marked in red.

Figure S2: Maps of the Eastern Himalayas indicating the occurrence in the IBAs included in this study of projected climate conditions outside of the range used to fit the species distribution models. Projections of these climate conditions were “clamped (see text for details). IBAs that were clamped are filled with red, and the intensity of the colour shows the proportion of the IBAs cells that were affected (as indicated by the colour bar).

Figure S3: Maps of the Lower Mekong indicating the occurrence in the IBAs included in this study of projected climate conditions outside of the range used to fit the species distribution models. Projections of these climate conditions were “clamped” (see text for details). IBAs that were clamped are filled with red, and the intensity of the colour shows the proportion of the IBAs cells that were affected (as indicated by the colour bar).


Change extremely likely
No consensus
A2
A1B
B1
2085
2055
2025
Number of Species
300
200
100
0
−30
−20
−10
0
10
20
30
Change in Availability of Suitable Climates, ΔPk (Number of IBAs)


−40
−30
−20
−10
no consensus
+10
+20
+30
+40
Diversity Change (2085)
N
500 km
N
500 km
A2
A1B
B1
2085
2055
2025
Number of IBAs
300
200
100
0
−40
−20
0
20
40
Diversity Change (Number of species)


0%
20%
40%
60%
80%
100%
% Species Turnover (2085)
N
500 km
N
500 km
A2
A1B
B1
2085
2055
2025
Number of IBAs
300
200
100
0
0 20 40 60 80 100
% Species Turnover