Land-use change interacts with climate to determine elevational species redistribution

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Climate change is driving global species redistribution with profound social and economic impacts. However, species movement is largely constrained by habitat availability and connectivity, of which the interaction effects with climate change remain largely unknown. Here we examine published data on 1464 elevational range shifts from 43 study sites to assess the confounding effect of land-use change on climate-driven species redistribution. We show that baseline forest cover and recent forest cover change are critical predictors in determining the magnitude of elevational range shifts. Forest loss positively interacts with baseline temperature conditions, such that forest loss in warmer regions tends to accelerate species' upslope movement. Consequently, not only climate but also habitat loss stressors and, importantly, their synergistic effects matter in forecasting species elevational redistribution, especially in the tropics where both stressors will increase the risk of net lowland biotic attrition.
Human activities during the Anthropocene have transformed most of the planet, of which global forest loss and climate change are considered among the greatest threats to global biodiversity\textsuperscript{1–5}. In response to these ongoing global changes, species are shifting their distributions to track suitable ecological niches along several geographic dimensions including latitude, longitude, and elevation/depth\textsuperscript{6–8}. Due to the widely-recognized positive spatial autocorrelation signal of temperature conditions along latitudinal (it is warmer in the tropics and cooler towards the poles) and elevational/bathymetric (it is warmer at low elevation/depth and cooler at high elevation/depth) gradients, broad patterns of latitudinal and elevational/bathymetric range shifts are frequently linked to climate change effects\textsuperscript{9–11}. For instance, Chen et al.\textsuperscript{12} calculated the velocity of species range shifts for a large set of species\textsuperscript{16}. Besides, small-scale species movements such as elevational range shifts could be largely constrained or confounded by local habitat availability\textsuperscript{17}–\textsuperscript{19}.

However, like temperature conditions, land use can also be positively autocorrelated in space\textsuperscript{13,14}, especially in mountain ecosystems where forest cover is not randomly distributed along elevational gradients (Fig. 1 and Supplementary Methods). The predominance of anthropogenic activities/disturbances in the lowlands\textsuperscript{13} and the harsh climatic conditions prevailing at treeline\textsuperscript{15} constrain the proportion of forest cover per elevational band to peak at mid elevations (Fig. 1a). This pattern suggests that directional forest cover change (e.g., intensive deforestation in lowland areas common in Southeast Asia or forest expansion after land abandonment at high elevations in Europe) may be confounded with climate change when studying patterns of elevational range shifts for a large set of species\textsuperscript{16}. Besides, small-scale species movements such as elevational range shifts could be largely constrained or confounded by local habitat availability\textsuperscript{17}–\textsuperscript{20}.

Hitherto, very few empirical studies have looked into interacting effects between climate change and land-use change on the magnitude and direction of species range shifts\textsuperscript{21–23} despite a wide recognition of potential synergistic and antagonistic effects\textsuperscript{24–26}.

Based on a recent and exhaustive review\textsuperscript{7}, we updated and extracted data from a set of 39 studies on climate-driven species range shifts to relate the rate of elevational range shifts against habitat and climate variables capturing baseline conditions, as well as temporal changes (Fig. 2). Making use of a high resolution global forest cover and forest change dataset\textsuperscript{27}, as well as the CHELSA climate dataset\textsuperscript{28}, we generated consistent and comparable climate and land-use change indicators for each study to perform our analyses at two different resolution levels using either the data aggregated at the site level ($n = 43$; some of the 39 studies focused on several study sites that were treated independently here) or raw data at the species level ($n = 1464$). We found that apart from temperature changes and baseline temperature conditions, the rate of climate-related elevational range shifts is also affected by local habitat features such as baseline forest cover and recent forest cover change. The overall synergistic effects between climate and habitat change reveal the importance of considering multiple threats holistically when predicting biodiversity redistribution and for biodiversity conservation.

**Results**

**Aggregated analysis.** Among the different linear models tested (see Methods) to explain the rate of species elevational range shifts averaged at the site level ($n = 43$), the model selection procedure yielded three candidate models of competing interest according to the corrected Akaike information criteria (AIC\textsubscript{c})\textsuperscript{29} (cf. $\Delta$AIC\textsubscript{c} < 2) (Table 1). All three ordinary least-square (OLS) regression models yielded similar AIC\textsubscript{c} values ($\Delta$AIC\textsubscript{c} < 0.2) and Akaike weights ($\sim$0.3). One model in particular (Model 2 in Table 1), being the most parsimonious, had the simplest structure common to all candidate models explaining the majority of variation (OLS: $F_{4,38} = 5.76$, $R^2 = 0.31$, $P = 0.001$) (Table 2 and Supplementary Tables 1 and 2).

We found a consistent positive interaction effect (cf. synergistic effect) between forest loss and baseline temperature conditions across all three candidate models retained for the site-level analysis (Table 2), even after controlling for sampling effort in Model 2 (cf. sites weighted by the number of species included) (Supplementary Table 2). Under warmer baseline conditions and greater forest losses (e.g., in the tropics or lowland areas), species

**Fig. 1** Spatial autocorrelation signal of forest cover and temperature across elevation. **a** General pattern of forest cover (%) and temperature (°C) per 100 m elevational band for 140 global mountain ranges. **b** The associated autocorrelation function (ACF) displaying the elevational autocorrelation signal of the proportion of forest cover and temperature along the elevational gradient. Lines and shade each represent the mean and ± 0.5 S.D. boundaries. For details on calculation refer to Supplementary Methods.
tend to shift more rapidly towards higher elevations while under colder baseline conditions (e.g., in boreal regions or high elevation zones), the effect of forest loss is reversed: species tend to shift less rapidly along the elevational gradient and even towards lower elevations (cf. negative shift rates) (Fig. 3).

We found additional, but not consistent interactions in the other two OLS regression models (Table 1). The positive interaction between forest loss and baseline forest cover (Model 1) was not significant itself, although the overall $R^2$ was slightly improved (Table 2). The interaction term between forest loss and taxa type (Model 3) was marginally significant (Table 2) with elevational range shifts being lower in magnitude for plants than for animals under high forest loss (Supplementary Fig. 1).

This weak trend was likely driven by a single data point for animals under high forest loss (Supplementary Fig.1).

.level suggest increasing shift rates for species with higher baseline temperature conditions, and for greater elevational distance to the highest mountain summit within the study area. Although the data suggest that the magnitude of the elevational shift rate might be higher under denser baseline forest cover conditions, this effect was not significant (see the 95% confidence intervals crossing the zero line for “Cover” in Fig. 4). The data also suggest that the magnitude of the elevational shift rate might be affected by synergistic effects between climate change rate and baseline temperature, but these effects were also not significant (see the 95% confidence intervals crossing the zero line for “CCR” and

### Table 1 Candidate linear models on the site average shift rate

| Model | Variables | AICc | ΔAICc | Weight | $R^2$ |
|-------|-----------|------|-------|--------|------|
| 1     | Loss, Cover, T, Loss × T, Loss × Cover | 357.2 | 0.35  | 0.34   |
| 2     | Loss, Cover, T, Loss × T | 357.3 | 0.08  | 0.31   |
| 3     | Loss, Cover, T, Loss × T, Type, Loss × Type | 357.3 | 0.16  | 0.36   |

Candidate linear models with interactive effects between climate and habitat features on the site average shift rate (n = 43), ranked by the corrected Akaike information criteria (AICc). T: baseline temperature, Loss: forest loss percentage, Cover: forest cover percentage, Type: taxa type (animal or plant).

### Table 2 Model details for the site average shift rate

| Parameter | Estimate | Std. error | t value | Pr (>|t|) |
|-----------|----------|------------|---------|----------|
| Model 1   | Intercept | 11.24      | 2.46    | 4.58     | <0.001   |
|           | scale (Loss) | −5.80      | 2.93    | −1.98    | 0.06     |
|           | scale (Cover) | 6.85       | 2.69    | 2.54     | 0.02     |
|           | scale( T) | 12.94      | 3.24    | 3.99     | <0.001   |
|           | scale (Loss) × scale (T) | 19.98     | 4.52    | 3.53     | 0.001    |
|           | scale (Loss) × scale (Cover) | 5.84      | 3.61    | 1.62     | 0.11     |
| Model 2*  | Intercept | 11.09      | 2.51    | 4.43     | <0.001   |
|           | scale (Loss) | −7.78      | 2.71    | −2.87    | 0.007    |
|           | scale (Cover) | 5.87       | 2.68    | 2.19     | 0.03     |
|           | scale (T) | 11.61      | 3.20    | 3.63     | <0.001   |
|           | scale (Loss) × scale (T) | 15.79     | 4.62    | 3.42     | 0.002    |
| Model 3   | Intercept | 8.68       | 2.97    | 2.92     | 0.006    |
|           | scale (Loss) | −3.36      | 3.25    | −1.04    | 0.31     |
|           | scale (Cover) | 6.99       | 2.64    | 2.65     | 0.01     |
|           | scale (T) | 13.60      | 3.21    | 4.24     | <0.001   |
|           | Type_plant | 2.88       | 4.62    | 0.62     | 0.54     |
|           | scale (Loss) × scale (T) | 18.16     | 4.76    | 3.82     | <0.001   |
|           | scale (Loss) × Type_plant | −9.75     | 4.44    | −2.20    | 0.03     |

Details of the three best fitting models (Table 1) for the site average shift rate (n = 43). Predictor variables are scaled (cf. the scale() function in R) for comparison purposes.

*See Supplementary Tables 1 and 2 for unscaled estimates and weighted coefficients of model 2, the most parsimonious model.

T: baseline temperature, Loss: forest loss percentage, Cover: forest cover percentage, Type: taxa type (animal or plant)
Discussion

We found evidence for the confounding impacts of habitat features (e.g., forest cover, forest loss) on climate-related species range shifts across elevation using both an aggregated (site level) and a disaggregated (species level) approach. At the site level, we found a robust and consistent synergistic effect between baseline temperature conditions and forest loss across all models. Although forest loss in colder regions of the world is likely to impede species upslope movements, potentially by interrupting habitat connectivity19, this negative effect is somewhat reversed in warmer regions where high forest loss tends to increase the elevational shift rate towards higher elevations. The mechanisms behind this synergistic effect of lowland deforestation on climate-driven upslope range shifts in warm environments are not yet known but may involve direct population extirpation of plant species, drastic microclimatic changes (e.g., increasing temperature and decreasing humidity) following habitat disturbance21,26,31,32 and, ultimately, local extinction at the lowest margin of species’ elevational ranges33. This result supports suggestions of rapid upslope range shifts through lowland biotic attrition34, especially in tropical lowland areas experiencing both warm temperature conditions and the most severe contemporary human disturbance impacts in terms of deforestation13,27.

In both analyses (i.e., aggregated and disaggregated), the generally positive effects of forest cover (although not significant at the species level) on the elevational shift rate reveal the importance of habitat cohesion and availability for species’ movement under climate change impacts18,20,24. The fact that warm-adapted species tend to shift more rapidly upslope compared to those in cooler regions could be explained by seasonal temperature stability, i.e., they need to move greater elevational distances to reach the suitable and very stable environment to which they are narrowly adapted to and which corresponds with their restricted thermal niches35,36. Alternatively, it could also be partially driven by the shallow temperature gradient across latitude in the tropics, which makes latitudinal shifts less likely than elevational shifts towards mountain summits34. The rate of climate change over time is not a major predictor in most models, likely due to the low spatial resolution of climate data, especially for mountainous regions. However, we did observe a positive interaction between forest loss percentage and climate change rate for the disaggregated analysis, when restricted to forest systems. Overall, the above-mentioned interactions emphasize the fact that isolating the effects of co-occurring stressors and ignoring their potential synergistic or antagonistic effects could be misleading21,25.

The elevational distance to the highest mountain summit within the study area was also found to be an important factor in explaining upslope shift rates at the species level: the greater the elevational distance to the highest summit, the more rapidly species shifted their range upslope. This finding supports the idea that limited physical space may constrain the rate of species’ range shifts along elevational gradients16,37,38. In addition, microclimate conditions and soil nutrition levels determined by montane mass (the Massenerhebung effect) could also limit species range extension39,40.

One limitation to our work lies in the short time-span of the forest data used (2000–2015), especially given that most selected studies covered periods of several decades. On average, initial surveys were conducted 44 years prior to the period covered by the Global Forest Watch database. Land-use history over the last decade is not likely to accurately mirror changes over previous decades, and this mismatch in time scale might have contributed to the unexplained variance in our models at the species level (cf. 87.4% on average, with ± 0.97% S.D.). Nonetheless, the spatial consistency that the Global Forest Watch dataset offers is a breakthrough for large-scale comparisons in habitat features (see discussion on model limitations using various habitat data
Sources of data were obtained from a variety of databases, including the National Nuclear Data Center (NNDC), the United Nations Framework Convention on Climate Change (UNFCCC), and the Global Atmosphere Watch (GAW) database. The data were collected from various locations around the world, including the Arctic, the Antarctic, and various regions in the tropics and subtropics. The data were then processed and analyzed using statistical software to determine the trends and patterns in the data.

The analysis revealed that there was a significant increase in the amount of carbon dioxide (CO2) in the atmosphere, with a corresponding increase in the temperature of the Earth. This increase in temperature has led to a variety of changes, including an increase in the rate of sea-level rise, changes in precipitation patterns, and changes in the distribution of plant and animal species.

The data also showed that the rate of change has been accelerating over time, with the rate of increase in CO2 doubling every 10 years from 1960 to 2010. This acceleration in the rate of change is likely to have significant implications for the future of the planet, with the potential for significant impacts on human societies, economies, and ecosystems.
focus on forest loss solely as it better reflects the dynamic of habitat disturbances. To account for the nested design of our disaggregated dataset (cf. several range shift values for a given single study site) and the potential pseudo-replication issue of having identical values for the set of variables available only at the study site level (e.g., climate change rate), we ran linear mixed-effect models (LMMs) with “Site” as a random factor potentially affecting the intercept (i.e., $\hat{\beta}_0$) and the slope parameter of the elevation-specific variables (i.e., $\hat{\beta}_1 + \text{Cover|Site} + 1 + \text{Cover + Loss|Site}$, as well as additive combinations including $1 + \text{Cover|Site} + 1 + \text{T + Loss|Site}$ and $1 + \text{Cover + Loss|Site}$). We used the “$\text{Imer}$” function from the `lme4` package in R to run LMMs. The optimal random component structure among the previously mentioned structures was determined by comparing AIC values of LMMs fitted by restricted maximum likelihood (REML), while the fixed effects were kept constant with all possible explanatory variables and two-way interaction terms incorporated (cf. the “beyond optimal model” sensu Zuur et al.51). Using REML is generally considered to give better estimates for the parameters51. We also calculated the model averaged coefficients and their bootstrapped confidence intervals to assess goodness of fit of the top model (Supplementary Fig. 7). All analyses were performed in Rsstudio59.

**Sensitivity analysis restricted to forest systems only.** To test whether the forest change data we used could adequately represent elevational habitat changes in general, we reran the above analyses at both site (n = 59) and species (n = 1120) levels on forest systems only, by restricting data to locations with average forest cover greater than 25%, and to sites with no fewer than 5 species resurveyed. Results were largely consistent with those across the entire forest cover gradient (Supplementary Table 6 and Supplementary Fig. 2).

**Data availability.** Supplementary Data 1 is the data used for site-level analysis, and Supplementary Data 2 for species-level analysis. Both datasets are available on Dryad [https://doi.org/10.5061/dryad.k8g2672].

**Code availability.** R script for running the analyses are available as Supplementary Software.

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**Author contributions**

T.C.B. and F.G. conceived the project; F.G. compiled the database with input from J.L., F. G., T.C.B., and J.L. analyzed the data and F.G. wrote the first draft of the paper with substantial contributions from T.C.B. and J.L.

**Additional information**

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