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# Global loss of climate connectivity in tropical forests

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# Abstract

Range shifts are a crucial mechanism enabling species to avoid extinction under climate change[1,2]. The majority of terrestrial biodiversity is concentrated in the tropics[3], including species considered most vulnerable to climate warming[4], but extensive and ongoing deforestation of tropical forests is likely to impede range shifts[5,6]. We conduct a global assessment of the potential for tropical species to reach analogous future climates – 'climate connectivity' – and empirically test how this has changed in response to deforestation between 2000 and 2012. We find that over 62% of tropical forest area (~ 10M km$^2$) is already incapable of facilitating range shifts to analogous future climates. In just 12 years, continued deforestation has caused a loss of climate connectivity for over 27% of surviving tropical forest, with accelerating declines in connectivity as forest loss increased. On average, if species' ranges shift as far down climate gradients as permitted by existing forest connectivity, by 2070 they would still experience 0.77°C of warming under the least severe climate warming scenario, up to 2.6°C warming for the most severe scenario. Limiting further forest loss and focusing the global restoration agenda towards creating climate corridors are global priorities for improving resilience of tropical forest biotas under climate change.

**200/200 words**

# Main text

Species survived periods of past climate warming by shifting their distributions polewards or upslope. Today, species are again moving as the world warms[1,2], but must now also contend with fragmentation of natural habitats by anthropogenic land-use change[7]. The tropics are of particular concern, being simultaneously the stronghold of most remaining terrestrial biodiversity[3] and the main source of new agricultural land[8]. Additionally, the tropics will experience the earliest appearance of novel climates[9], for which many tropical species will be unequipped because of narrow thermal safety margins[4] and limited dispersal relative to rates of climate change[10,11].

The potential for a species to shift its range in response to climate change depends both on the future availability of suitable habitat with an analogous climate, and on the connectivity between that habitat and the species' current distribution[12]. Many studies have addressed these factors individually, but few have integrated them to quantify the connectedness of natural areas to future climate analogues – hereafter: 'climate connectivity'[13]. Of those studies that do[6,12,14], none has applied the approach pan-tropically, nor considered how climate connectivity has changed over time.

Here we combine a high-resolution forest cover layer[15] with current and projected future Mean Annual Temperature[16] (hereafter: temperature), to quantify across the tropics: (1) the potential for species to reach analogous future climate within existing forest cover (year: 2012), and (2) the change in climate connectivity from 2000 to 2012, during a period of extensive deforestation. Climate connectivity was calculated using the method of McGuire et al.[6], whereby natural land cover – here defined as cells with more than 50% forest cover[15] – was partitioned into patches based on current temperature (~1950-2000; WorldClim v1.4), and each forest patch traced to the coolest patch that could be reached by traversing a gradient of hotter to cooler adjacent patches. All patches were then assigned mean future temperature for the year 2070 (average for 2061-2080), derived from the HadGEM2-AO general circulation model[17] and Representative Concentration Pathway (RCP) 8.5, which is the most severe ('business-as-usual') IPCC scenario. To capture the extent to which forest cover enables species to reach somewhere that, under future climate warming, is the same or cooler than their current locations, climate connectivity was calculated as the current temperature of each patch minus the future temperature of its designated destination patch. Negative values indicate that the coolest reachable forest is still warmer under climate change than the current temperature, and species now living in the source patch would fail to reach an analogous climate under projected warming.

We found that, on average, if tropical species shifted as far along temperature gradients as permitted by current forest cover, they would still experience 2.6°C of warming under projected future climate change (median value across all realms; Figure 1a). By comparison, average warming without any movement would be 4°C. Average climate connectivity was generally higher for larger land masses ($F = 45.5$, $p < 0.001$; Supplementary Figure 14), and varied by biogeographic realm ($F = 78.5$, $p < 0.001$; Figure 2a): the Neotropics and Afrotropics were the least well connected, resulting in unavoidable warming of 2.9°C and 2.8°C, respectively. Range-shifting species in Indomalaya, Australasia and Oceania would also fail to reach analogous temperatures, experiencing warming of 2.6, 2.4 and 2.2°C, respectively. Thus, the average tropical forest, for any given realm, is not sufficiently connected along a temperature gradient to enable species to avoid climate change by shifting their distribution.

Overall, 62% of tropical forest area failed to achieve successful climate connectivity ($\geq 0$; median value across realms), whereby species' range shifts within existing forest cover could circumvent climate warming. This figure is comparable to the 59% observed in the continental United States by McGuire et al.[6], and is all the more concerning because of the greater numbers of climate-vulnerable species in the tropics. Variation across biogeographic realms showed slightly different patterns than for average climate connectivity ($F = 9.94$, $p < 0.001$; Figure 2b; considering only land masses with < 100% failure). Indomalaya was the least successful realm with 70.1% of its forested area failing to connect to climate analogues, followed by the Neotropics (66.8%), Afrotropics (62%), Oceania (57.8%), and Australasia (37.4%). As in previous studies[12,14], regions with large, contiguous forest patches connecting warmer lowland regions to cool uplands, such as the western Amazon, Congo Basin and New Guinea (Figure 1a), can compensate somewhat for low average climate connectivity. That said, in these locations the total path distance from source to target patch was often substantial – up to 2,820 km for one source patch in the Neotropics. Climate connectivity was consistently low for regions with severe and extensive loss of lowland rainforests, such as Indochina, Brazilian Atlantic forest and West Africa[8,18].

In only 12 years, change in climate connectivity was widespread – 26.6% of cells forested in 2000 or 2012 (~ 4M $km^2$) experienced loss of climate connectivity, compared to 10% of cells that experienced gains (Figure 1b). While average climate connectivity did not differ between years ($F = 0.791$, $p = 0.374$; Figure 2a), the proportion of forested area that was successfully connected decreased overall from 2000 to 2012 ($F = 13.6$, $p < 0.001$; Figure 2b), with variation between realms ($F = 19.9$, $p < 0.001$; Figure 2b). The largest losses of climate connectivity were seen in Indomalaya (-32.2%), followed by the Neotropics (-19.5%), Australasia (-3.17%), and Oceania (-1.64%). Conversely, there was a considerable gain of connected forest area in the Afrotropical realm (+17.6%), likely driven by forest gain in central Africa[15].

Loss of climate connectivity from 2000 to 2012 increased non-linearly with increasing area of forest loss ($F = 57$, $p < 0.001$; Figure 3; considering only land masses with > 0% forest loss), and the shape of the relationship varied between realms ($F = 99.2$, $p < 0.001$; Figure 3). Acceleration of climate connectivity loss with expanding deforestation is an inevitable and concerning consequence of successively removing links between forest patches[5]. Observed patterns were, however, shallower than under random deforestation (see Supplementary Methods 6), which suggests that concentrating forest loss in certain areas, akin to land sparing[19], is a better way to maintain regional climate connectivity than peppering the landscape with small-scale deforestation.

Reversal of the losses in climate connectivity already observed requires reinstating patch connections, particularly along climate gradients[20]. This objective could be achieved through forest restoration initiatives such as the Bonn Challenge, which aims to restore 3.5 million $km^2$ by 2030. Habitat corridors are not appropriate for all taxa and locations[21,22], but could be of particular value in locations where poor climate connectivity (Figure 1a) or high connectivity loss (Figure 1b) coincide with high species' vulnerability to climate change (Supplementary Figure 15)[23] or high levels of endemism (Supplementary Figure 16).

The climate connectivity metric used here is a measure of the physical potential for thermally restricted species to track climate through near-contiguous forest cover[6]. We focus on broad trends across the Earth's most biodiverse terrestrial region, which requires assumptions and simplifications that render our results less applicable at finer spatial scales and for particular species[24]. We do not incorporate any species-specific information, but suggest that loss of climate connectivity increases the risk of extinction for thermally sensitive species, which includes many tropical forest specialists that operate close to their upper thermal limits[25] and have limited potential for physiological adaptation[26]. Tropical ectotherms are already exposed to maximum operative temperatures that are, on average, 17°C above their upper thermal limits[4], and must therefore rely on microhabitats and behaviour to avoid overheating. Other factors, such as phenological shifts[27] and dispersal limits[28], will also affect the need and capacity for species to shift their ranges.

We assumed that forest patches of 10 km$^2$ and above would be sufficiently large to facilitate species range shifts, but in reality minimum patch size will depend on the species of interest. Some mobile species could overcome patch fragmentation through long-distance dispersal across the unsuitable matrix. However, in doing so they may incur other fitness costs, such as reduced food intake and increased predation risk[29], such that loss of connectivity will nonetheless be detrimental. High elevation patches might also be inherently vulnerable because there are fewer places that are cooler. Repeating our analyses with different minimum patch sizes and for high and low elevation patches separately revealed qualitatively similar results (Supplementary Methods 1 and 2, respectively).

Our estimates of climate connectivity are conservative because the forest cover layer does not distinguish between natural forest and tree plantations[15]. A precautionary reanalysis excluding tree plantations for the seven countries where plantation boundaries were available (Brazil, Cambodia, Colombia, Indonesia, Liberia, Malaysia, and Peru) revealed similar results, except that from 2000 to 2012 the percentage of forest failing to connect to analogous climates decreased by 2.9% when including plantations, compared to an increase of 8.7% if they were excluded (see Supplementary Methods 3). We do not use sub-canopy temperature nor account for variation in forest quality, but note that thermal buffering by forest canopy varies little between pristine and degraded forests[30]. Relative temperature change in the understorey, and thus our broad conclusions, should therefore be consistent across forest types.

We focus on the most severe climate warming scenario (RCP8.5), which appears the most likely outcome[31]. Repeating our analysis for the least severe scenario (RCP2.6) resulted in similar overall trends, although the proportion of successfully connected forest was enhanced and the loss of climate connectivity alleviated under RCP2.6 (Supplementary Methods 4). Other climate variables – particularly temperature extremes and precipitation – are important in determining the climatic niche of any given species. Unfortunately, projections of future precipitation under climate change remain highly uncertain[17,32] and are highly variable in space, making it difficult to determine the gradient that species would follow to avoid deleterious changes in precipitation.

Our study quantifies climate connectivity throughout the tropics and over time. Loss of forest cover is extensive in the tropics[8,15] and causes widespread and accelerating fragmentation of remaining habitat[5]. Simultaneously, climate change poses an increasing risk to thermally restricted tropical species[4]; the ability of these species to track climate will be important in determining their risk of extinction under climate change. We found that, across most of the tropics, current forest cover is insufficient to facilitate range shifts to future climate analogues, and is likely to worsen as forest loss continues. Landscape planning for climate resilience should limit the extent of forest loss to protect existing forest cover, via land-sparing approaches and carbon-based payments for ecosystem services. Where opportunities arise to protect or restore forest, such as through the global landscape restoration agenda, disproportionate gains may come from connecting forest along climate gradients[20].

**1751/2000 words**

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# Methods

We focused our study pan-tropically, including all land masses located between ±23.4° latitude. For those land masses with a true extent beyond the tropics, boundaries were buffered by 100 km to reduce artificial truncation of climate gradients[6]. Maps were analysed at 1-km resolution projected into the World Cylindrical Equal Area projection. All spatial layers were processed with Python code implemented using the arcpy module in ArcMap Version 10.4.1[33].

## Climate-partitioned forest patches

Since we were interested in climate connectivity for species inhabiting tropical forests, we calculated climate connectivity based on movement along a temperature gradient within forested areas only. We defined cells as forest or non-forest using tree cover data from Hansen et al. 2013[15]. For the year 2000, cells were defined as forested if they had > 50% tree cover[15]. Results are conservative because the Hansen et al. dataset does not differentiate between natural forest and tree plantations, but see Supplementary Methods 3 for analyses excluding cells within tree plantations for those countries where plantation boundaries were available (Brazil, Cambodia, Colombia, Indonesia, Liberia, Malaysia, and Peru). For the year 2012, cells were classified based on forest loss and forest gain[15] relative to forest cover in 2000. If a cell had experienced forest loss from 2000 to 2012, it had gone from a forested to non-forested state and the cell was classed as non-forest in 2012. Conversely, if a cell had experienced forest gain from 2000 to 2012, it had gone from a non-forested to a forested state; providing there had been no concomitant loss, the cell was classed as forest in 2012. Summary statistics for forest cover in 2000 and 2012 by biogeographic realm can be found in Supplementary Table 4.

We partitioned forest patches using a present-day (~1950-2000), 30-arc-second global layer for Mean Annual Temperature (hereafter: temperature) from the WorldClim database Version 1.4[6,16], re-sampled to 1 km$^2$. The same approach was applied separately to forest cover in 2000 and 2012: temperature values were assigned to forested cells and reclassified to increments of 0.5°C (full range: -18 to 32°C), based on evidence that tropical species are sensitive to this degree of temperature difference[34,35]. The resulting raster was converted to polygons, whereby neighbouring forest cells with the same reclassified temperature value were assigned to the same polygon (hereafter: forest patch). While our approach is not specific to any particular taxon, it may be helpful to consider the method in the context of range shifts by non-volant terrestrial animals[13]. We removed forest patches < 10 km$^2$, based on the assumption that they could not support a population for long enough to enable range shifts. See Supplementary Methods 1 for the implications of varying minimum patch size. Patches within 2 km of each other and with the same temperature were aggregated, conservatively assuming that populations could move across 2 km of non-forest to reach suitable habitat[6]. See Supplementary Methods 5 for the implications of preventing patch aggregation across major rivers and roads.

## Climate connectivity

The logic behind the measure of climate connectivity in McGuire et al.[6] is that it represents the maximum temperature differential between current and future conditions that can be achieved by traversing a gradient from hotter to cooler patches within existing natural habitat. We assigned mean current and future temperature to all forest patches, again using data from WorldClim. Future temperature was for the year 2070 (average for 2061-2080), derived from the HadGEM2-AO general circulation model[17] and Representative Concentration Pathway (RCP) 8.5, which is the most severe (‘business-as-usual’) IPCC scenario. See Supplementary Methods 4 for a re-analysis using RCP2.6, the least severe IPCC scenario.

To trace each forest patch to its final destination, we identified which patches were neighbours, and iterated over all unique temperatures from cooler to hotter, each time identifying the patch corresponding to that temperature and the identity of its coolest neighbour. For patches with no cooler neighbours, the final destination patch is assigned as itself. For all other patches, the destination is assigned as the final destination of its coolest immediate neighbour. This algorithm ensures that the coolest destinations are passed on with each iteration, enabling destination patches to extend beyond immediate neighbours. See Supplementary Methods 7 for a full worked example[6], and Supplementary Figure 13 for a schematic diagram.

Once each origin patch has a designated final destination patch, climate connectivity is calculated as the temperature difference between them. The key question is whether forest cover is sufficient for organisms to reach a place that, under future climate warming, is the same as or cooler than their current location. Thus, climate connectivity is the current temperature of the origin patch minus the future temperature of the destination patch. Where the value is zero or positive, the patch has achieved successful climate connectivity: there is sufficient structural connectivity between forested areas for organisms to reach forest that is same as or cooler than the temperatures they currently experience. Negative values indicate that the coolest reachable forest is still warmer under climate change than the current temperature, and inhabitant organisms would fail to reach an analogous climate under projected warming.

## Statistical analyses

All data were analysed in R (version 3.5.2)[36]. The specific variables included are detailed below. For all models, statistical significance was inspected by dropping each fixed effect in turn and comparing to the full model[37]. The significance of main effects involved in an interaction was assessed in the same way, except reduced models were compared to a full model without the interaction term.

## Current state of climate connectivity

Climate connectivity was necessarily calculated at a patch-level, but because patches themselves were not constant through time our spatial unit of replication was land mass. There were 697 land masses in total, comprising whole islands, such as Borneo and Madagascar, as well as sections of continents clipped to the extent of the tropics, such as for Africa and Australia. To assess current status we calculated median climate connectivity for each land mass, as well as the proportion of the total area of forested patches that failed to achieve successful climate connectivity (i.e. climate connectivity < 0).

Median climate connectivity (range -3.8-0°C; n = 1394) and percentage area of unsuccessful connectivity (range 16-100%; n = 88) were modelled against year (categorical: 2000 or 2012) and biogeographic realm (categorical: Neotropics, Afrotropics, Indomalaya, Australasia, and Oceania), with an interaction between them. Model-predicted values with confidence intervals are summarised in Supplementary Tables 5 and 6. Median climate connectivity models also included (log) land mass area as an explanatory variable, fit using a Generalized Additive Model (GAM) in the mgcv package[38]. Area of unsuccessful connectivity was modelled as a binary variable (sum patch area with climate connectivity < 0 versus sum patch area with climate connectivity ≥ 0) using a Generalized Linear Model (GLM) with a quasi-binomial error distribution to account for overdispersion, fit using the lme4 package[39]. For these models we assessed only land masses with < 100% of forest area classed as unsuccessful in either year, which reduced the sample size to the extent that we were unable to include land mass area as an additional explanatory variable.

## Change in climate connectivity

Change of climate connectivity from 2000 to 2012 was first calculated at the level of the grid cell. For both years, we created a binary raster of climate connectivity, where cells were either successful (climate connectivity $\geq 0$) or unsuccessful (climate connectivity $< 0$). Change was then calculated as climate connectivity in 2012 minus climate connectivity in 2000, and could take one of three values: no change (value of 0), loss of climate connectivity (value of -1), or gain of climate connectivity (value of 1). Where cells changed from a forested to a non-forested state, we assume a loss of climate connectivity for that cell. Where cells changed from a non-forested to a forested state (e.g. via secondary forest regrowth on abandoned farmland)[40], we assume a gain of climate connectivity for that cell. For analyses, loss of climate connectivity was captured for each land mass by the proportion of the total area of forested cells (forested in 2000, 2012 or both) that experienced a change from successful to unsuccessful climate connectivity. An analogous approach was applied to quantify gain of climate connectivity.

Area of connectivity loss was modelled as a binary variable (area losing connectivity versus area not losing connectivity), for land masses with > 0% forest loss between 2000 and 2012 ($n = 400$). Explanatory variables were: biogeographic realm and (log + 1) area of forest lost between 2000 and 2012. We used a Generalized Additive Model (GAM) implemented in the mgcv package[38], with a quasi-binomial error distribution to account for overdispersion. See Supplementary Methods 6 for a comparison of observed patterns of connectivity loss compared with 100 null scenarios.

**1453/3000 words**

## Code Availability

Custom Python code to calculate climate connectivity can be downloaded from GitHub (https://github.com/rasenior/ClimateConnectivity). These scripts have been directly adapted from the methods in McGuire et al.[6], and the R code therein (https://github.com/JennyMcGuire/ClimateConnectivity).

## Data Availability

Pan-tropical climate connectivity data that support the findings of this study have been deposited in The Environmental Information Data Centre (EIDC) and are accessible at [PENDING REF].

## Methods References

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# End Notes

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## Author Contributions

R.A.S. and D.P.E conceived the study. R.A.S., D.P.E., and J.K.H developed the methods, with R.A.S. writing scripts to calculate climate connectivity and performing statistical analyses. R.A.S. wrote the first draft of the manuscript, with contributions from D.P.E. and J.K.H.

## Conflicts of Interest

Authors declare no conflicts of interest.

## Figure Captions

Figure 1 **Maps of current climate connectivity and change in climate connectivity over time.** Panel a shows climate connectivity in 2012, with positive values in blue indicating successful connectivity and negative values in red indicating unsuccessful climate connectivity. Panel b shows the change in climate connectivity from 2000 to 2012, where positive values in blue indicate a gain of connectivity and negative values in red a loss of connectivity. To aid visualisation we have shifted and magnified land masses in Oceania.

**79/100 words**

Figure 2 **Climate connectivity of land masses in different biogeographic realms.** Climate connectivity in the year 2000 is represented by green circles and in 2012 by orange triangles. Panel a shows results for median climate connectivity, with the dashed line indicating zero climate connectivity at and above which successful climate connectivity is achieved. Panel b shows results for the proportion of total forested area that fails to achieve successful climate connectivity. Solid points in panels a and b are model-predicted values with 95% confidence intervals; dotted lines in panel b indicate 95% confidence intervals that extend beyond 0 or 100%. Raw data in panels a and b are plotted in the background as semi-transparent points.

**112/100 words**

Figure 3 **The proportion of total forested area in each land mass that lost climate connectivity between 2000 and 2012.** Connectivity loss (% area) is plotted against increasing area of forest loss on a log10 scale and across different biogeographic realms. Neotropics = orange, Afrotropics = blue, Indomalaya = green, Australasia = yellow and Oceania = pink. Points correspond to raw data, with point size indicating the number of observations at that value. Fitted lines derive from model predictions with 95% confidence intervals. **81/100 words**