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Deforestation poses deleterious effects to tree-climbing species under climate change

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Habitat loss poses a major threat to global biodiversity. Many studies have explored the potential damages of deforestation to animal populations but few have considered trees as thermoregulatory microhabitats or addressed how tree loss might impact the fate of species under climate change. Using a biophysical approach, we explore how tree loss might affect semi-arboreal diurnal ectotherms (lizards) under current and projected climates. We find that tree loss can reduce lizard population growth by curtailing activity time and length of the activity season. Although climate change can generally promote population growth for lizards, deforestation can reverse these positive effects for 66% of simulated populations and further accelerate population declines for another 18%. Our research underscores the mechanistic link between tree availability and population survival and growth, thus advocating for forest conservation and the integration of biophysical modelling and microhabitat diversity into conservation strategies, particularly in the face of climate change.

Habitat loss, including that through deforestation, is currently the biggest threat to living species across all taxa[1,2]. As of 2019, global forests comprised 32% of their estimated pre-industrial land area[1], and every year, another 10 million hectares of forests are cut down globally[3]. Deforestation severely reduces biodiversity[4–6], most obviously affecting populations of exclusively arboreal species that fully rely on trees for daily life[7]. For both fully and partially arboreal species, however, deforestation may also reduce food, shelter from predators or opportunities for thermoregulation[8,9]. Many lizards, for example, thermoregulate by climbing and moving around the trunks of trees[10–12]. Yet we still lack a mechanistic understanding of how deforestation might cause population declines by reducing the availability of microhabitats and thus an organism's ability to thermoregulate. This knowledge gap reduces the efficacy of conservation and restoration planning for many species of concern[13].

Exacerbating the impacts of habitat loss, global climate change is making many regions warmer and drier and increasing the frequency and intensity of extreme climate events[14]. Species can respond to these changes through shifts in distribution or phenology[15–19], and by modifying their behaviour[11,20]—for example, by moving around tree trunk microhabitats to thermoregulate[21]. However, no study has yet theorized how the combined effects of deforestation and climate change might reduce the availability of key microhabitats, and thus accelerate population declines.

To address these gaps, we simulated the combined effects of tree loss and climate change on diurnal terrestrial ectotherms that are semi-arboreal, use behaviour to escape stressful thermal conditions, and are predicted to rely heavily on thermoregulation to deal with changing climates[11,22]. Specifically, we simulated the behavioural thermoregulation of lizards (that is, behaviours used by animals to regulate their body temperature, for example, by shifting between microhabitats) and tracked their preferred microhabitat, thermal opportunity, energy budgets, and population trends with and without access to trees. We used a tree trunk temperature model[23,24] to calculate trunk surface temperatures at different shade conditions and heights above-ground under past (1980–2000) and projected future (2080–2100) climates—the latter under a high greenhouse gas emissions scenario. We then determined how losing access to trees would impact lizard populations, given their biophysical limitations and requirements[25–28] and the constraints of microhabitats. For these latter data, we used a published set of hourly North American microclimates over a large latitudinal and longitudinal climatic gradient from warm deserts to

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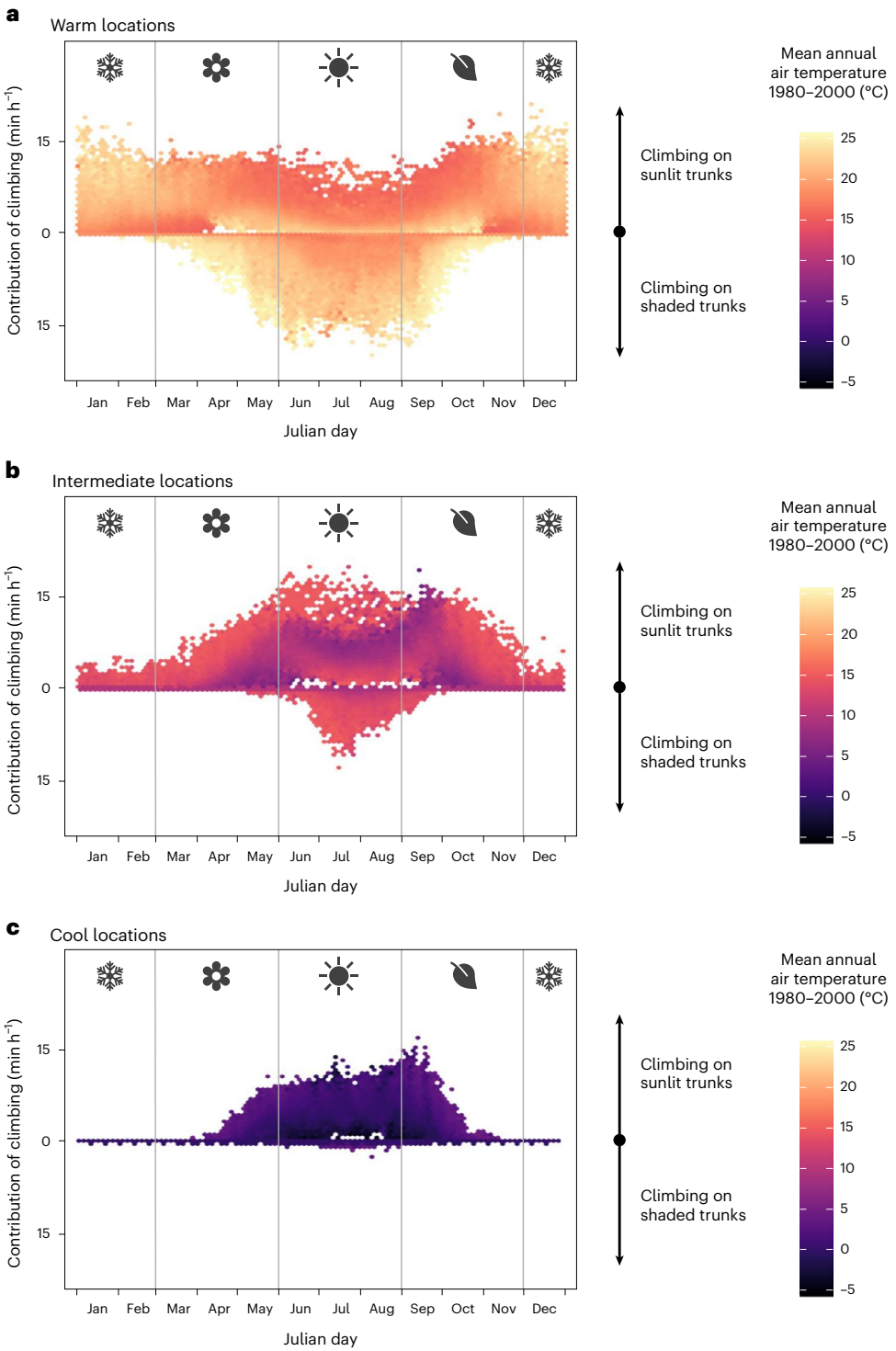

Fig. 1 | Climatic gradients determine the thermoregulatory importance of tree trunks to ectotherms throughout the year. a–**c**, We divided our locations into three tertiles based on their mean annual temperature: warm climate (mean annual temperature: 17.36 ± 3.51 °C) (**a**), intermediate climate (mean annual temperature: 8.04 ± 2.35 °C) (**b**) and cool climate (mean annual temperature: −0.26 ± 2.34 °C) (**c**). For each Julian day, the plots show the mean number of minutes per hour when lizard activity was dependent on sunlit tree trunks (positive direction) or shaded tree trunks (negative direction). The colour of each hexagon in the plot represents the average air temperature of locations sharing the same *x* and *y* values; grey vertical lines and associated icons indicate the seasons.

temperate forests and subtropical habitats[29]. The climatic gradients of North America and the relatively high resolution of the microclimatic data (36 km and 1 h spatial and temporal scales, respectively[29]) enabled us to examine the efficiency of behavioural thermoregulation under various climates, microenvironment conditions (with and without trees; Extended Data Fig. 1) and climate scenarios (past and future projected climate).

Tree trunks as a thermoregulatory resource

To optimize body temperature, our simulated lizards preferred to spend substantial time on tree trunks. Across our spatial domain, simulated lizards used trees to both cool down and warm up, and tree trunk usage shifted seasonally (Fig. 1). In almost all locations (97.7%), lizards primarily used trees to bask and warm, especially in cooler locations and seasons (Fig. 1), by climbing on sunlit trunks during mornings and

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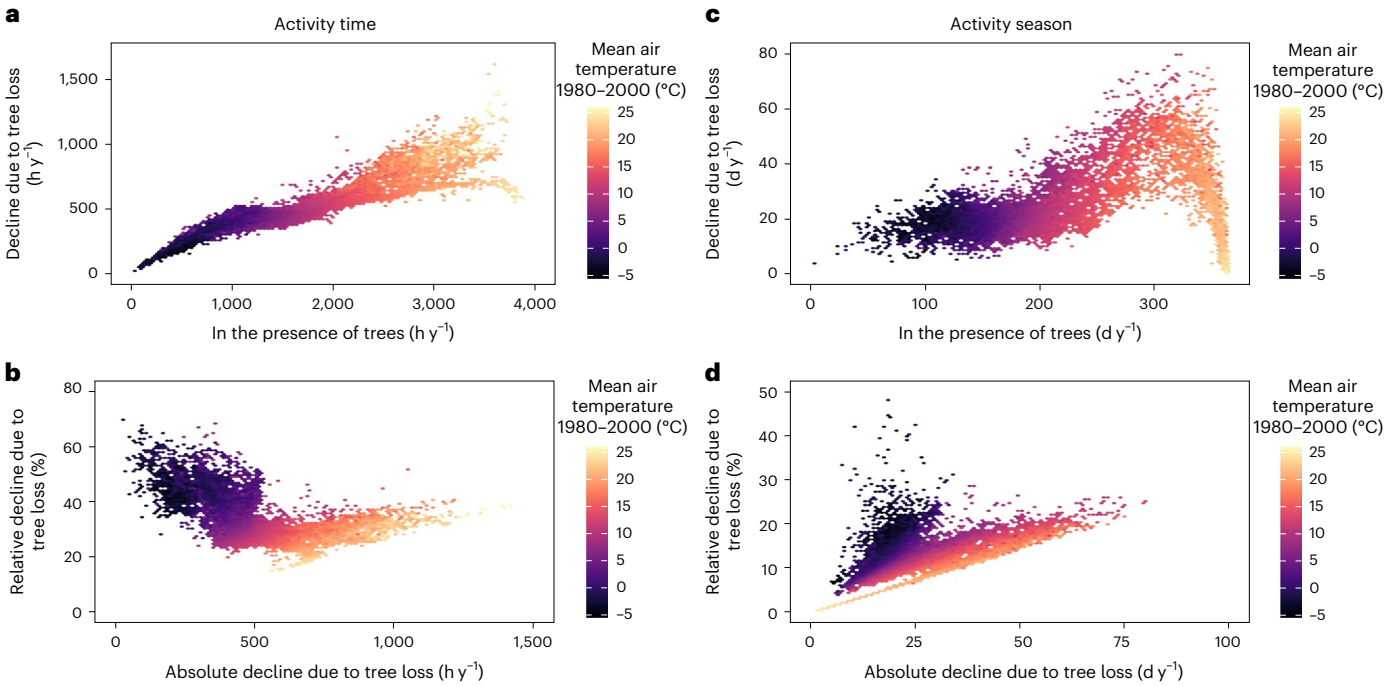

Fig. 2 | The effect of tree loss on annual activity time and length of activity season depends on climate conditions. a–**d**, In cool locations, lizards lose fewer absolute hours (**a**) and days (**c**) of activity than lizards in warmer locations but a relatively larger portion of their already small available hourly (**b**) and daily (**d**) thermal opportunity. Data are presented using years 1980–2000. The colour of each hexagon in the plot represents the average air temperature of locations sharing the same *x* and *y* values.

evenings (Extended Data Figs. 2 and 3) although basking opportunities were available on the ground. Thus, our model suggests that at these early and late hours of the day, lizards may choose to bask on vertical trunk rather than sunlit horizontal ground surfaces to optimize their positioning relative to the sun's rays in ways that maximize the absorption of shortwave radiation, an important factor for thermoregulation (Supplementary Figs. 1 and 2).

Climbing lizards use trees to deal with different thermoregulatory challenges, extending their available activity time. Under warm conditions, simulated lizards preferred to climb on shaded trees rather than use shaded ground, mainly during the hotter midday period (Extended Data Fig. 3), and especially in warm locations during the warm season (Fig. 1). When we examined the optimal height for thermoregulation, we found that lizards from warm locations must climb higher tree trunks to escape warm conditions near the ground and to maintain preferred body temperatures for activity (Extended Data Fig. 4). By climbing higher, lizards can maximize heat loss through both convection (due to lower air temperature and higher wind velocity) and conduction (due to lower trunk temperatures) (Supplementary Figs. 3 and 4). Climbing high, however, might come with an energetic cost due to the additional physical effort required for climbing and maintaining grip on trunk surfaces[30]. Lizards experiencing cooler conditions struggle more to sufficiently increase body temperature for activity[31,32], and in these cooler conditions climbing is a critical thermoregulatory strategy that enables them to achieve higher body temperature than on the ground[33,34]. When the sun is lower on the horizon (as in winter or in cool climates), the sun's rays are more effectively used for basking when the lizard is vertical against the tree (compared with horizontal on the ground). Overall we suggest that reforestation efforts should enable lizards access to both sunlit and shaded microhabitats over short distances; overplanting could limit lizards' ability to access sunlit trunks, reducing thermal opportunity[10]. Our results also show that lizards from warm locations need taller trees for thermoregulation, whereas shorter trees or bushes may be sufficient in cooler locations.

The impact of tree loss

To examine the effect of deforestation or tree loss on populations, we disabled the ability of the simulated lizard to climb trees. In this condition, lizards were only able to thermoregulate on sunlit or shaded horizontal ground (Extended Data Fig. 1). Our model suggests that tree loss causes an average decline of 34 ± 8% (mean ± s.d.) in the activity time of lizards across North America. Lizards from warm locations suffered a greater loss of thermal opportunity compared with those from cooler locations when we considered *absolute* declines in activity time (Fig. 2a and Extended Data Figs. 5b, 6b,d and 7a). However, when we considered *relative* declines in activity time, we found that loss of trees led to a 50% decrease in activity and a collapse of thermal opportunity in cooler locations, where lizards highly depend on tree trunks to more effectively absorb solar radiation (Fig. 2b and Extended Data Figs. 5c, 6c,e and 7b).

In our simulation, tree loss also reduced the number of days that lizards could be active (Fig. 2c,d)—thus shortening the reproductive season and leading to fewer clutches and population decline[35]. We found that simulated lizard populations from moderately warm locations (with a mean air temperature of 8–18 °C) experienced the largest decline in seasonal activity, losing 32.72 ± 13.52 (mean ± s.d.) days per year (Fig. 2c). As the lizards are unable to bask on trees during the cooler periods of the year, their activity season shrinks to a warmer part of the year. In contrast, in the warmest locations (with a mean air temperature above 20 °C), where year-round activity is possible, tree loss is predicted to cause a much smaller change in the length of the activity season—a reduction of 11.16 ± 10.74 days per year. In the coolest locations (with a mean air temperature below 2 °C), the activity season is already ~50% shorter compared with that in warmer locations (127.49 ± 23.46 days versus 248.61 ± 73.08 days in all other locations), and tree loss shortens the activity season by a further 18.81 ± 4.07 days.

Our results suggest that deforestation can lead to lizard population declines via two mechanisms, that is, by reducing (1) total activity time (that is, diminished foraging and energy gain) and (2) the number

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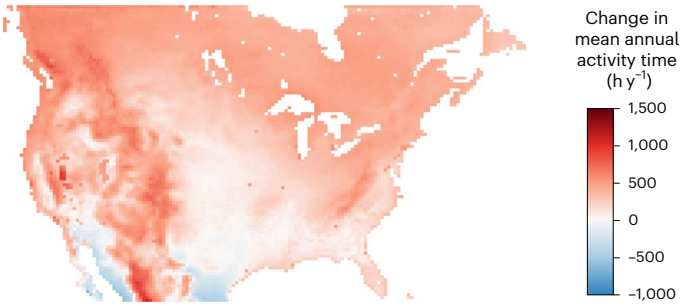

Fig. 3 | Latitudinal gradients of the impacts of climate change on hourly thermal opportunity. For ectotherms, such as lizards, the effects of climate change will be mostly positive. For some locations at lower latitudes, annual average activity time will decrease due to an increase in the number of hours that are too warm for activity.

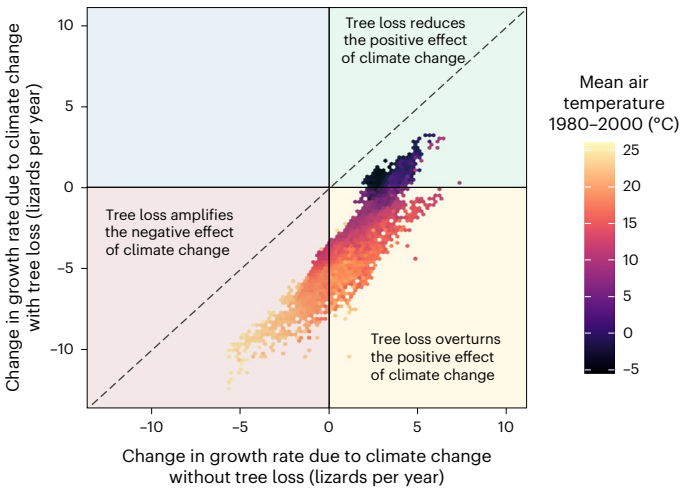

Fig. 4 | The predicted change in growth rate due to climate change with and without tree loss. Tree loss is projected to worsen the effects of climate change on population growth rate. The plot area is split into four subareas based on the division of locations presented in Table 1. The brown area represents locations where growth rate will decline both with and without tree loss. Both the green and yellow areas represent locations where tree loss negatively affects population growth rate, whereas climate change affects it positively. In the green area, the positive effect of climate change is stronger than the negative effect of tree loss (that is, the net effect is positive). In the yellow area, in contrast, the positive effect of climate change is weaker than the negative effect of tree loss (that is, the net effect is negative). The colour of each hexagon in the plot represents the average air temperature of locations sharing the same *x* and *y* values. The diagonal dashed line represents equal effect of climate change on growth rate with and without tree loss.

of days in the activity season (that is, diminished energy gain and shortened reproductive season). The predominant mechanism by which population declines occur varies geographically. In cool locations, both mechanisms act simultaneously and may lead to population collapse. In these locations, thermal opportunity is highly cold limited, even with trees, and will further decline if lizards lose the ability to bask on trees. In moderately warm locations, populations will mostly suffer from shortening of the activity season, whereas at the warmest locations the activity season may remain extensive but the loss of trees as thermal shelter during hot conditions would cause declines in the potential daily activity time.

Unfortunately, reduced activity time and seasons are not the only risks posed by deforestation. Deforestation, and tree loss in general, is likely to drive local extinction for arboreal species and habitat fragmentation, increased disease transmission, altered trophic cascades and higher exposure to predators for other species[36–38]. The reduced thermal opportunities we show here are likely to be magnified and compounded by these additional effects. For example, deforestation is one of the main factors causing declines in insect populations, which constitute the diet of many animals[39]. Lizards and other ectotherms in deforested areas would therefore not only have less foraging time but also less abundant prey. This example illustrates that the potential impacts of tree loss cannot be considered singularly, and models can be further improved by accounting for myriad complex interactions.

The impact of climate change

The impacts of climate change differ among lizard populations from warm or cold locations. In most locations, warming due to climate change increases potential activity time for lizards, resulting in a net positive effect on their populations. This is especially the case in cold locations in mountainous areas or at higher latitudes (Fig. 3). However, in the warmest locations, activity time is predicted to decrease in response to warming, decreasing population growth rates (Supplementary Fig. 5). Climate change is also predicted to affect the length of the activity season of lizards (Supplementary Figs. 6 and 7). In the warmest locations, where the activity season for lizards is year round, a bimodal activity pattern emerges in our simulation, with lower activity levels during the summer (Supplementary Figs. 6 and 7). In cooler locations, the activity season for lizards would extend by approximately 1–3 months as winters shorten and the spring and autumn seasons warm.

These phenological trends align with previous predictions in which ectotherm populations in many locations with cool to mild climates are predicted to benefit from climate change, whereas populations at warm locations will be more at risk[27,40]. Importantly, our model does not consider the full life cycle of lizards and therefore does not account for the high risks that more extreme and frequent heat events under climate change might bring to lizard embryos[27]. Therefore, our model is probably a conservative estimate of the negative effects of climate change, especially in warm locations.

Our model also predicts changes in lizard climbing behaviour due to climate change. In most locations, warming due to climate change will decrease the time that lizards spend basking on tree trunks and will increase the time and energy spent escaping heat. Lizards are predicted to increase the time spent on the shaded parts of tree trunks and, as ground temperatures warm, they will need to climb higher up the trunk to escape the heat (Supplementary Fig. 8). These changes in climbing behaviour must be considered when planning conservation and restoration programmes to ensure that trees of the appropriate height are available.

The combined effect of tree loss and climate change

Our deforestation model shows that tree loss may exacerbate, reduce or even overturn the effect of climate change on ectothermic populations under different climate scenarios (Fig. 4, Table 1 and Extended Data Fig. 8). For 66% of lizard populations, tree loss will overturn any positive effect of climate-change-induced warming, making climate change predictions negative. For 18.2% of lizard populations, mainly from the warmest locations, tree loss will exacerbate reductions in population growth rates by 5.04 ± 0.89 lizards per year. For the remaining 15.8% of populations, located mainly in the coolest locations, tree loss will reduce the positive effects of climate change on population growth rates by 2.85 ± 0.51 lizards per year. Table 1 shows the distribution of each outcome of deforestation, the mean air temperature associated with each outcome, and the change in population growth rate due to climate change alone and climate change together with tree loss. Our calculations suggest that enabling a higher percentage of lizards to access trees is likely to counter the negative effects of climate change, especially in warmer locations. Therefore, we suggest that conservation

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Table 1 | A summary of the three possible outcomes of climate change when lizards lose access to trees

Group colour	Trend	Population (%)	Mean air temperature in 1980–2000 (°C)	Effect in the presence of trees (lizards per year)	Effect in the absence of trees (lizards per year)
Green		15.8	−0.04±3.46	3.43±0.64	0.58±0.47
Brown		18.2	18.29±3.77	−1.09±1.08	−6.13±1.57
Yellow		66	7.67±6.23	2.09±1.01	−1.91±1.61

The group colours correspond with the colours used in Figs. 4 and 5, and represent different outcomes with and without tree loss: green, both outcomes are positive; brown, both outcomes are negative; and yellow, positive outcomes in the presence of trees but negative outcomes under the tree loss scenario. For each outcome, we calculated the percentage of populations from all the populations in our analysis, mean air temperature (in the years 1980–2000) and the mean effect of climate change on growth rate, in the presence and absence of trees (values presented as mean±s.d.). The size of each arrow represents the magnitude of the effect of climate change. The left arrows represent the presence of trees; right arrows represent the absence of trees.

programmes in such areas should be more conservative in permitting tree loss and more proactive in tree planting and restoration (Extended Data Fig. 9).

Our results indicate that most climbing ectotherms will only benefit from climatic warming if they have access to trees for thermoregulation. Without access to trees, populations in historically moderate climates will decline (yellow area in Fig. 4), whereas the benefit from climate change to populations in historically cooler climates will be diminished (green area in Fig. 4). Therefore, we suggest that conservation and habitat restoration efforts target these locations in which the availability of trees plays the most crucial role.

Although our study domain includes regions with scarce trees, such as North American deserts, we still assessed tree loss impacts across the entire area. Our calculations suggest that populations in areas with abundant trees are more sensitive to deforestation than those in areas with scarce trees. Specifically, 78.8% of locations in which deforestation is predicted to overturn the positive effects of climate change have more than 10% tree cover. Even when we excluded treeless locations from our model, 67% of the remaining populations are predicted to lose any thermal gains of climate change through deforestation (Supplementary Fig. 9 and Supplementary Table 5).

Even without deforestation, the warmer and drier conditions predicted under climate change may cause widespread regional declines in vegetation cover, which should be considered when prioritizing areas for conservation and restoration. In a previous study[29], a dynamic vegetation model[41] was used to simulate changes in green vegetation cover across North America due to climate change and it was found that large areas of forests, savannas and shrublands will suffer from loss of vegetation cover by 2080–2100, especially during the summer and autumn seasons. To find which populations are most sensitive to these declines, and to identify areas for conservation, we compared the predicted change in vegetation cover by 2080–2100[29] to this study's predicted effects of tree loss on the population growth rates of lizards (Fig. 5). We found that the predicted vegetation loss will often occur in areas where our model predicts that climbing is crucial for effective thermoregulation in changed climates. In particular, loss of vegetation cover is predicted to occur for 43.3% of the populations where tree loss amplifies climate-change-induced declines (brown points in Fig. 5) and 55.6% of the populations where tree loss negates the positive effects of climate change (yellow points in Fig. 5). We suggest that conservation efforts should focus on such locations, and especially for the latter populations, where conservation could support population growth in the presence of climate change. We also found that the most severe vegetation loss will occur in warm locations where availability of trees may not be able to stop population declines (brown area in Fig. 4, brown points in Fig. 5). In these locations, climate change will not only introduce new and warmer climates but also reduce tree cover needed for climbing and thermoregulation, hence leading to a more severe decline in ectotherm populations.

Although we focused on a lizard as a model animal, our conclusions are relevant to myriad animals that climb trees and whose habitats are at risk from deforestation worldwide. For example, out of 6,657 lizard species listed in ref. 42, 2,068 species (31%) were defined as exclusively or partially arboreal, and out of 776 mammal species listed in ref. 43, 307 species (40%) were defined as fully or partially arboreal. Species that are exclusively arboreal are at high risk of extinction under full deforestation[44]. For both fully and partially arboreal species, our model suggests that climbing may be an important thermoregulatory behaviour. This has been shown in many species beyond lizards. Koalas, for example,

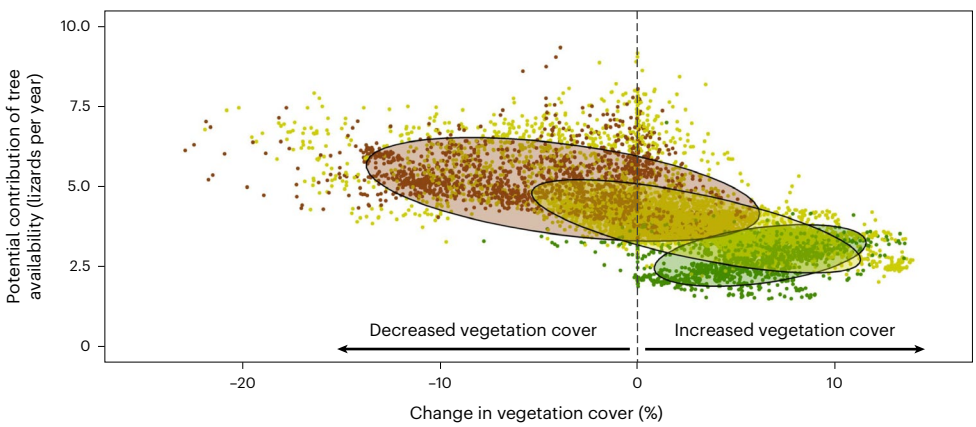

Fig. 5 | Climate change is predicted to decrease the percentage of green vegetation cover in locations where populations are more vulnerable to tree loss. The *x* axis represents predicted change in vegetation cover by 2080–2100, as predicted by ref. 29. The *y* axis represents the predicted decrease in population growth rate due to tree loss, as predicted in this study. Each point represents a location in our North American domain. The points are coloured according to the areas presented in Table 1 and Fig. 4. The ellipses surround the central 90% of the points of each group.

use the cool surface of tree trunks for cooling during warm ambient conditions[21], and *Littorina irrorata* snails climb *Spartina alterniflora* stems to cool down[45]. By accounting for the thermoregulatory needs of vulnerable species, we can better predict how these species will respond to climate change and habitat alteration and develop targeted conservation strategies and habitat management efforts to preserve populations, biodiversity and ecosystem health.

Conclusions

Many animals, particularly ectotherms, rely on thermoregulation to maintain suitable body temperatures[46]. Thermoregulation can be done more efficiently if habitats contain a large number of microenvironments that the animal can shuttle between to reach its preferred body temperature[20,47]. In the face of climate change, it is even more crucial to maintain spatial variety in habitats as animals will have to deal with more extreme conditions, and finding thermally suitable microhabitats will be even more challenging[11,48]. Trees make habitats more complex and enrich the microenvironments available for thermoregulation. Tree clearing and deforestation simplify or homogenize habitats, decrease the variety of microenvironments inside these habitats and therefore reduce opportunities for behavioural thermoregulation, suggesting that previous models, in which thermoregulation was limited to the ground[11,25–28,49], have underestimated the activity time of animals with climbing ability.

By combining a biophysical model with high-resolution climate data, we showed the critical role of habitat preservation, and specifically that of tree trunks, for mediating the impacts of climate change on climbing animals. Tree loss, even before considering climate change, is predicted to reduce the activity time of climbing lizards, decrease population growth rates and shorten the activity season. All these effects show different patterns along the climatic gradient of the tested domain.

Our simulations emphasize the value of preserving climbing elements—even when trees are absent or lost—for optimal heat gain in cool conditions and heat loss in warm ones. During warm time periods, animals may use the shade cast by vertical climbing surfaces, such as rocks[50,51], and man-made elements, such as walls and utility poles[52], but rocks or man-made structures may not be tall enough for optimal cooling under warm conditions. Without trees, competition for these alternatives will increase and the warmer the conditions become, the greater the competition for taller microhabitats will be.

Tree loss accelerates the negative effects of climate change on lizards and reduces the potential positive effects. Although warming due to climate change may have net benefits to many North American lizard populations, these benefits require the preservation of trees. Deforestation causes reduced population growth rates for lizards across North America, and declines in vegetation cover due to climate change[29] are expected to amplify the negative effects of tree loss in these areas. Our work provides a new hypothesis for the mechanisms by which tree trunks contribute to ectotherm population growth or declines and for the likely effects of tree clearing and deforestation on ectotherm populations in the face of climate change. Here we show the far-reaching importance of the tree trunk microenvironment for lizards, especially when considering projected warming due to climate change. We believe that these predictions should be considered when planning conservation and restoration projects to provide animals with the unique habitat structure they need.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41558-024-01939-x.

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Methods

General approach

We explored the effects of tree loss using an energy-balance model that simulates a thermoregulating lizard. Our model is based on Buckley's[53] model that later was expanded in refs. 25–28. We calculated tree trunk temperatures and compared the activity times, energy budgets and population growth rates of (1) lizards that can thermoregulate by climbing trees and (2) lizards that have no access to trees. To explore how different climate conditions may affect the importance of trees, and how climate change may affect the impacts of tree loss, we conducted our analysis using the North America domain for both past climate (1980–2000) and future climate (2080–2100) scenarios, assuming the representative concentration pathway (RCP) 8.5 emission scenario[54]. Here the biophysical model from ref. 27 was translated into the popular programming language Python[55].

Microclimate data and tree trunk temperatures

We parameterized our models of climbing and non-climbing lizards using a published set of hourly microclimates[29]. The microclimates represent United States, south Canada and north Mexico at a resolution of 36 km × 36 km for the past (1980–2000) and the future (2080–2100), assuming a radiative forcing of +8.5 W m^{-2} at year 2100. Every hour in the dataset includes the microclimate conditions needed to calculate the operative temperature of lizards, such as ground temperature, air temperature and radiation at ground surfaces ranging from 0% to 100% shade.

To calculate the operative temperatures of climbing lizards, we expanded the dataset to include microclimates on vertical tree trunks. We developed an energy-balance model based on refs. 23,24 and parameterized it using our microclimate data. The R code of the model is available in the accompanying Zenodo repository[55]. Here we detail how we fed the microclimates from ref. 29 into the model, describing only those features relevant to our calculations of microclimate.

Trunk temperature calculation. At each time step, we solved for trunk temperatures that balance the energy budget:

$$R_{net} = H + LE + S, \tag{1}$$

where R_{net} is the net radiation (W m^{-2}) at the bark–air boundary, H (W m^{-2}) is the flux of sensible heat, LE (W m^{-2}) is the flux of latent heat (assumed to be negligible for trunk temperatures) and S (W m^{-2}) is the flux of heat stored in the trunk. Radiation is positive towards the trunk, and all other surface fluxes have positive values when directed away from the trunk. To enable lizards to experience how trunk temperature may vary along a tree trunk, we calculated trunk temperatures for every height above the ground. Note that we assumed no latent heat effect on trunk temperatures, as in refs. 24,56.

Net radiation. The net radiation R_{net} is calculated as

$$R_{net} = R_s + R_l, \tag{2}$$

where R_s (W m^{-2}) and R_l (W m^{-2}) are the net solar and longwave radiations absorbed by the trunk, respectively. R_s was calculated using the shortwave flux towards the trunk (S_t, W m^{-2}), reflected solar radiation towards the trunk from the ground (S_r, W m^{-2}), diffuse solar radiation (S_d, W m^{-2}), the ground albedo (α_g, dec. %, between 0 and 1) and the trunk albedo (α_t, dec. %):

$$R_s = (1 - \alpha_t)(1 - SHD)(S_t + S_r) + S_d \tag{3}$$

SHD indicates whether the microhabitat is an open (0) or shaded (1) microhabitat. We used the SWDOWN variable[29] to calculate S_t, S_r and S_d. First, we used the insol R package[57] to calculate the zenith angle (θ, degrees) of the sun using the *sunvector* function, and the diffuse ratio (D_r, dec. %) and clear sky irradiance (S_c, W m^{-2}) using the *insolation* function. Next we calculated the cloud fraction (CLD, dec. %) by dividing the downwards beam radiation by the amount of radiation expected under clear sky:

$$\mathrm{CLD} = \frac{\mathrm{SWDOWN}}{S_c \times \cos(\theta)} \tag{4}$$

Next we calculate S_t, S_r and S_d:

$$S_t = \mathrm{CLD} \times S_c \times (1 - D_r) \times \sin(\theta), \tag{5}$$

$$S_d = \mathrm{CLD} \times S_c \times D_r \tag{6}$$

and

$$S_r = \mathrm{CLD} \times S_c \times (1 - D_r) \times \mathrm{ALBEDO} \times \sin(\theta), \tag{7}$$

where ALBEDO is the ground albedo from ref. 29.

Net longwave radiation. The net flux of longwave radiation (R_l, W m^{-2}), the difference between incoming and outgoing longwave radiation, depends on the current trunk temperature (T_{tr}, K), longwave flux from the sky (L_{atm}, W m^{-2}), ground temperature (T_g, K), canopy temperature (T_v, K), and emissivities of the ground (ϵ_g, 0.95 dec. %), vegetation (ϵ_v, 0.96 dec. %) and trunk bark (ϵ_t, 0.96 dec. %). We assumed that the view factor for upward and downward radiation is 50%, hence the net longwave radiation in the tree trunk is:

$$R_l = 0.5L_{up} + 0.5L_{down} + 3\epsilon_t\sigma T_{tr}^4, \tag{8}$$

where σ is the Stefan–Boltzmann constant (5.67×10^{-8} W m^{-2} K^{-4}), L_{up} and L_{down} are the longwave radiations from above and below the trunk, respectively, and $3\epsilon_t\sigma T_{tr}^4$ is the linearization of the net radiation formula around the trunk. For simplicity, we assumed that half of the L_{up} radiation arrives from the tree leaves and half from the sky, calculated as

$$L_{up} = 0.5\epsilon_t L_{atm} + 0.5\epsilon_t\epsilon_v\sigma T_v^4 \tag{9}$$

$$L_{down} = \epsilon_t\epsilon_g\sigma T_g^4 \tag{10}$$

Sensible heat flux. The flux of sensible heat (H) was calculated as a function of the coefficient for sensible heat (c_h, W m^{-2} K^{-1}), trunk temperature (T_{tr}, K) and air temperatures near the trunk (T_{air}, K):

$$H = c_h(T_{tr} - T_{air}) \tag{11}$$

where c_h is the convective heat transfer coefficient, calculated as the sum of forced- and free-convection components as described in ref. 23, and T_{air} is the air temperature near the trunk, using the TAIR variable from ref. 29, for each height in the dataset and for either 0% or 100% shade.

Heat mass flux in trunk. The flux of heat mass in the trunk (S) was calculated as

$$S = \frac{\beta(T_{tr} - T_{tr(t-1)})}{\Delta t}, \tag{12}$$

as in ref. 56, where β is the trunk heat mass (J K^{-1} m^{-2}), Δt is the model time step (720 s) and the numerator contains the temperature difference (K) between current and previous time steps.

Solving for trunk temperature. Equation (1) was solved by Newton–Raphson's method of iteration. First, we calculated the solar radiation absorbed by the trunk, which is independent of trunk temperature. Then we performed five iterations of the model. In the first iteration, R_{net}, H and S are calculated from the trunk temperature at the preceding hour. At each iteration, the updated trunk temperature was calculated as

$$T_{tr} = \frac{h_0 - r_0 + hm_0}{r_1 - h_1 - hm_1}, \quad (13)$$

where

$$h_0 = -c_h T_{air} \quad (14)$$

$$h_1 = c_h \quad (15)$$

$$r_0 = R_{net} \quad (16)$$

$$r_1 = -4\epsilon_t \sigma T_{tr}^3 \quad (17)$$

$$hm_0 = -S \quad (18)$$

$$hm_1 = \frac{\beta}{\Delta t} \quad (19)$$

R_{net}, H and S were then updated according to the new T_{tr}.

Other parameters used in the simulation are in Supplementary Table 1. For simplification, we assumed a constant trunk radius of 20 cm. Although the radius of an object is expected to directly impact its thermal inertia, ref. 56 showed that for trees, factors such as low thermal inertia and low conductivity of the trunks result in the bark surface temperature being primarily influenced by the external environment, with the trunk diameter having almost no effect.

Output parameters used in the biophysical model include the trunk temperatures in fully sunlit (0% shade) or fully shaded (100% shade) trunks at each height and the amount of solar radiation that is normal to the trunk. For each height, these conditions represent the range of the thermal conditions available for thermoregulation. These parameters were added as additional microclimates to the sunlit and shaded ground temperatures from ref. 29.

Operative temperature calculation

For each hour in the microclimate dataset, we calculated the operative temperatures across all available microhabitats, but under the scenario of tree loss, lizards were not able to exploit the microhabitats offered by trees. A summary of all the available microhabitats under each scenario is presented in Extended Data Fig. 1. Without deforestation, access to trees enabled lizards to exploit 14 types of microhabitats: the ground and 13 heights on a tree, ranging from 3 cm to 198 cm above the ground. Moreover, to enable lizards to thermoregulate in the shade, each microhabitat type (ground and tree trunk) was available with 0% shade or 100% shade. We also calculated the operative temperatures of lizards with two possible postures that either maximize (lying) or minimize (standing) conductive heat transfer. Under a tree-loss scenario, simulated lizards were able to access only the ground microhabitats. Thus, our model assumed that tree loss decreases the available possible combinations of operative temperatures from 56 (14 locations × 2 shade levels × 2 postures) to 4 (1 location × 2 shade levels × 2 postures).

For each of these possible combinations, the model calculates the operative temperature based on hourly air temperatures, radiative loads and wind speeds. We calculated these body temperatures as $T_{b,t} = T_{b,t-1} + \Delta T_b$, by solving heat-exchange equations in ref. 58, where $T_{b,t}$ (K) and $T_{b,t-1}$ (K) are the operative temperature during the current and preceding hours, respectively, and ΔT_b (K) is the calculated change in operative temperature between the two hours. We divided each hour into temporal steps of 120 s to yield small values of ΔT_b, which enhanced the stability of the model. The majority of the calculations, particularly for lizards on the ground, are similar to those used in ref. 27 and below we detail how we calculated the operative temperatures of active lizards on tree trunks. The temperature calculations of ΔT_b for each microhabitat and posture are described in Supplementary Table 2. We parameterized our lizard model using the characteristics of a semi-arboreal species, *Sceloporus undulatus*, which is diurnal, widespread across North America and inhabits a gradient of climatic conditions (Supplementary Fig. 10 and Supplementary Table 3). This species has been extensively studied[31,59–62], providing us with substantial knowledge of its thermal physiology, which is essential for parameterizing the biophysical model.

Solar radiation absorption. In the open (on ground or tree), the lizard absorbs both direct and scattered solar radiation, whereas in the shade it absorbs only scattered solar radiation[63] (see Supplementary Table 2 for a detailed description of the calculations). In our model, we assumed the surface area that absorbs the direct solar radiation (A_p, m^2) to be 40% of the total lizard surface area and the surface area that absorbs the scattered solar radiation (A_{ee}, m^2) to be $0.89 \times (A_L - A_C)$, where A_L (m^2) is the total surface area of the lizard and A_C (m^2) is the surface area of the lizard that is in contact with the surface. This calculation is also taken from ref. 63. See Supplementary Table 3 for detailed parameterization for the lizard model, and Supplementary Table 4 for a full list of parameter names and definitions.

Longwave radiation absorption and emission. At all microhabitats and shade levels, the lizard absorbs longwave radiation from the surface area that is exposed to the air (A_{air}, m^2). On the open ground, the lizard absorbs longwave radiation emitted from the ground surface (absorbed by the ventral surface area, A_{down}, m^2) and from the sky (absorbed by the dorsal surface area, A_{up}, m^2). On an open location on a tree, the lizard ventrally absorbs longwave radiation emitted from the tree trunk through A_{down}, and dorsally absorbs longwave radiation both from the sky and from the ground (each by half of A_{up}). For lizards in the shade, we replaced longwave radiation from the sky with radiation from the canopy, using the canopy temperature in ref. 29.

Convection coefficient. The last change we conducted in the operative body temperature calculations is in the calculation of the convection coefficient, h_L. Although previous models assumed a constant h_L when an animal is exclusively active on the ground, where free convection is assumed[26,27], for example, ref. 58, climbing lizards are more exposed to wind and therefore to forced convection. As forced convection varies with wind velocity, we calculated h_L for each height above the ground, using the corresponding air temperature and wind speed at that height, and the air density. The calculation was taken from the function *onelump* in the R package NicheMapR[64,65], translated into Python and inserted into our biophysical model.

From microhabitat selection to population growth rate

As previously mentioned, in each time step the model calculates all the possible operative temperatures for the lizard. During the daytime, the lizard chooses the microhabitat that minimizes the distance between the operative temperature and the preferred temperature, 33.1 °C (ref. 31). For each time step (120 s) during the daytime, the lizard can be active if its body temperature is in the range suitable for activity, between 29.4 °C and 36.3 °C (central 80% of field body temperatures[31]) and can therefore forage and gain energy[27]. If under all the possible conditions, the lizard's body temperature is lower or higher than the critical thermal minimum (CT_{min}) or maximum (CT_{max}), respectively (11.4 °C and 40.4 °C, respectively[62]), the lizard will burrow to a depth of 12 cm, at which time its body temperature equals that of the soil.

Once the lizard enters the burrow, it can emerge only if it senses a signal that it is thermally safe to come out. We defined this signal as a body temperature between CT_{min} and CT_{max}, and a rise (if it is cold) or a decrease (if it is hot) of at least 0.1 °C during the previous hour, as suggested in ref. 66. During the night, the lizard stays inactive on the ground or enters a burrow if conditions are colder than CT_{min}.

For simplicity, we did not explicitly model the thermal landscapes and the energetic costs of moving and searching for preferred temperatures, for example, refs. 47,67. Simplifications of this kind are plausible when studies simulate the impacts of climate change on large regions[11,25–28], for example, refs. 53,68,69, or the impacts of habitat loss[51]. Therefore, our work can be considered a best-case scenario in which the model's predictions highlight the importance of the existence of diverse microhabitats, rather than the importance of their abundance or the costs of moving between them. Furthermore, although our model did account for shuttling between sunlit and shaded microenvironments, and postural changes from lying to standing, it did not consider other potential behaviours. These behaviours include changing body orientation in response to the sun's rays and wind direction[49,64]. Nonetheless, our simulation encompassed locations with both maximum and minimum solar radiation (open and shaded microhabitats, respectively) and diverse wind speeds (higher and lower tree trunks, respectively), so choosing a different microhabitat (for example, with a different shade condition or wind speed) may compensate for the absence of the other behaviours.

To determine the feeding rates for each hour of foraging, we first calculated the maximal velocity (υ_{max}, m s^{-1}) of the lizard as

$$\log_{10}(\upsilon_{max}) = 0.044 + 0.2 \times \log_{10}(M_b), \quad (20)$$

based on published observations where M_b is the lizard's body mass[70]. We then calculated the actual velocity of the lizard, based on its body temperature (T_b)[71], as

$$\upsilon_{tot} = \upsilon_{max}((95.0 + (40.3 - 28.4)/5.0 \times (T_b - 28.4))/100) \quad (21)$$

Hence, the distance travelled in each second of foraging, d (m), equals υ_{tot}. To calculate the amount of energy consumed by the lizards at each time step[53], we assumed that (1) the energy content of an insect equals 30.2 J; (2) the rate of insect encounter, assuming foraging along a line equals 0.005 insects m^{-1} s^{-1} (refs. 59,72); (3) 50% of insects encountered are captured by a foraging lizard and (4) lizards assimilate 76% of ingested energy[31]. Hence, at each hour, the energy intake ($e_{i,h}$, J h^{-1}) is

$$\begin{aligned} e_i, h = {} & 30.2\ (\text{J insect}^{-1}) \times 0.005\ (\text{insects m}^{-1}\ \text{s}^{-1}) \\ & \times 0.5 \times 0.76 \times d\ (\text{m}) \times 3{,}600\ (\text{s h}^{-1}) \end{aligned} \quad (22)$$

The energy intake is then inserted into the gut, and foraging may continue in the simulation as long as there is free space in the gut. The maximum gut capacity, C_{max} (J), is a function of body temperature[31,53]. The energy found in the gut was assimilated by the lizards whenever they had food in their gut and body temperature was between 29.4 °C and 36.3 °C because digestion proceeds slowly at higher or lower temperatures[31]. For each hour, we calculated the digestive efficiency as

$$DE_h = \left\{ \sin\left[\frac{\pi\left(85.34 - 0.05 \times T_b + 0.000074 \times T_b^3\right)}{180} \right] \right\}^2 \quad (23)$$

At the end of each day, the mean digestive efficiency (DE, dec. %) and the amount of energy in the gut (J_{gut}, J) were used to calculate the mean energy gain of that day (E_{gained}, J d^{-1}) as

$$E_{gained} = DE \times J_{gut} \quad (24)$$

The energy expenditure was calculated for each hour separately, based on experimental studies of metabolic rate. The resting metabolic rate (RMR, J s^{-1}) was modelled as[61]

$$\ln(RMR) = -10.0 + 0.51 \times \log(M_b) + 0.12 \times T_b \quad (25)$$

We multiplied RMR by 1.5 to yield the RMR of a digesting lizard[73] and, for a foraging lizard, multiplied this rate by 2 (ref. 74). For each hour, we calculated the energy expenditure considering the relative time spent in foraging and time spent in rest. At the end of each hour, the hourly energy expenditure was subtracted from the total energy balance. At the end of each day, we added the energy gain from that day to the total energy balance.

Rates of population growth (r_0, lizards y^{-1}) were computed according to ref. 53:

$$r_0 = m \times e_{year} - \mu, \quad (26)$$

where e_{year} equals the annual net energy balance by an adult (J y^{-1}), μ equals the annual rate of mortality ($197.26 \times 10^{-5} \times 365$) and m equals the number of eggs produced per joule multiplied by the probability of surviving to adulthood (2.78×10^{-5}) (ref. 53).

Spatial analysis

We ran the simulation across a North American domain using published data on past and future microclimates[29]. We examined the contribution of climbing to the thermoregulatory behaviour of the lizard, and the impacts of climate change on this behaviour across 10,303 coordinates in North America. For each location, we calculated thermal opportunity as hours and days of activity per year, and the population growth rate under current and future climates, with and without deforestation.

For each location, we also calculated the minimum percentage of lizards that should have access to trees to prevent population declines under climate change using the following equation:

$$r_{\text{no deforestation}} \times p + r_{\text{deforestation}} \times (1 - p) = 0, \quad (27)$$

where $r_{deforestation}$ and $r_{no\ deforestation}$ are the changes in growth rate under climate change with and without deforestation, respectively, and p is the portion of the population with access to trees. After simple algebraic development, we calculated p as

$$p = \frac{r_{deforestation}}{r_{deforestation} - r_{no\ deforestation}} \quad (28)$$

Sensitivity analysis

As species vary in their thermal physiology and can acclimate to different conditions[75], we conducted a sensitivity analysis to examine the influence of our assumptions and species parameters on the simulation results. To do so, we increased, decreased, or both increased and decreased the lizard's body mass (±50%), minimum and maximum temperature for emergence (±50%), temperature range suitable for activity (±50%), solar absorptivity (to 65% absorptivity, assuming a lighter coloured lizard) and number of insects available (±50%). We then examined how each parameter impacted the effect of tree loss on annual population growth rates in the future (Supplementary Table 6), the effect of climate change on annual population growth rates without tree loss (Supplementary Table 7), the combined effect of both climate change and tree loss on the annual population growth rates (Supplementary Table 8), and the percentage of populations where deforestation will decrease the positive effect of climate change, amplify a negative effect of climate change, or overturn any positive effect of climate change (Supplementary Table 9). Our results were qualitatively similar across the various analyses, except when we increased the minimum temperature for emergence (that is, lizard activity is more

cold restricted) and changes in population growth rates remained positive for most of the locations even under the deforestation scenario (Supplementary Table 9), especially in cold locations (Supplementary Table 8).

We also examined how excluding locations with almost no trees may influence our results. For each location, we calculated the percentage of tree cover using published maps of evergreen or deciduous needleleaf trees, evergreen broadleaf trees, deciduous broadleaf trees, and mixed or other trees[76]. We then examined how excluding the locations that have less than 10% tree cover impacted our percentages of population trends (Supplementary Fig. 9 and Supplementary Table 5).

Data availability

The microclimates on the ground are available in ref. 29. Owing to its substantial size, the microclimate dataset of tree trunks is not available on a publicly accessible server. However, the data are available upon request. All model output data, including all the data needed for creating the figures and tables, are available from Zenodo at https://doi.org/10.5281/zenodo.10546868 (ref. 55).

Code availability

The original trunk temperature model, lizard model and all codes for data analysis and figure creation are available with the data from Zenodo[55]. Updates to the codebase are available at https://github.com/levyofi/Zlotnick_et_al_NCLIM_2024.

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Author contributions

O.B.Z. performed research and analysed data. O.L. designed research and provided mentorship. O.B.Z. and O.L. wrote the first version of the article. K.N.M. contributed new reagents/analytic tool. All authors contributed to writing of the final article.

Competing interests

The authors declare no competing interests.

Additional information

Extended data is available for this paper at https://doi.org/10.1038/s41558-024-01939-x.

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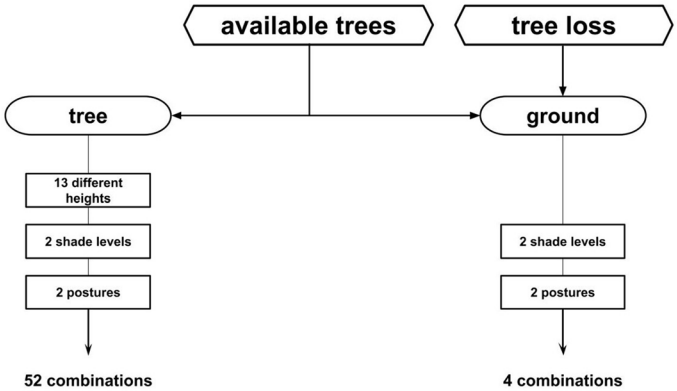

Extended Data Fig. 1 | A scheme of the microhabitats available for a simulated lizard. The availability of microhabitats differed between our two deforestation scenarios (with or without available trees). In the scenario with available trees, the lizard can exploit all the potential microhabitats in all postures (56 combinations of microhabitat, shade level, and posture). Under the scenario of tree loss, it can exploit only the microhabitats on the ground (4 combinations). This scheme applies only to daytime; at night, the lizard is limited to lying on the ground in 100% shade or entering a burrow.

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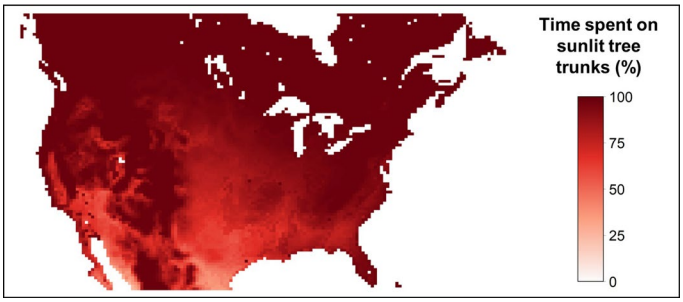

Extended Data Fig. 2 | Proportion of time spent on sunlit tree trunks. The predicted proportion of time spent on sunlit tree trunks when climbing was necessary for activity under current climate (1980–2000). Lizards predominantly climb on sunlit tree trunks rather than shaded ones, except in the warmest locations. The time of necessary climbing was defined as periods when the tree trunk was the only microhabitat enabling the lizard to reach its body temperature within the activity temperature range. Climbing on sunlit tree trunks showed a high correlation with basking behaviour, particularly when other microhabitats were too cold for activity. This suggests that lizards primarily use tree trunks as a warm retreat during colder periods of the year or day.

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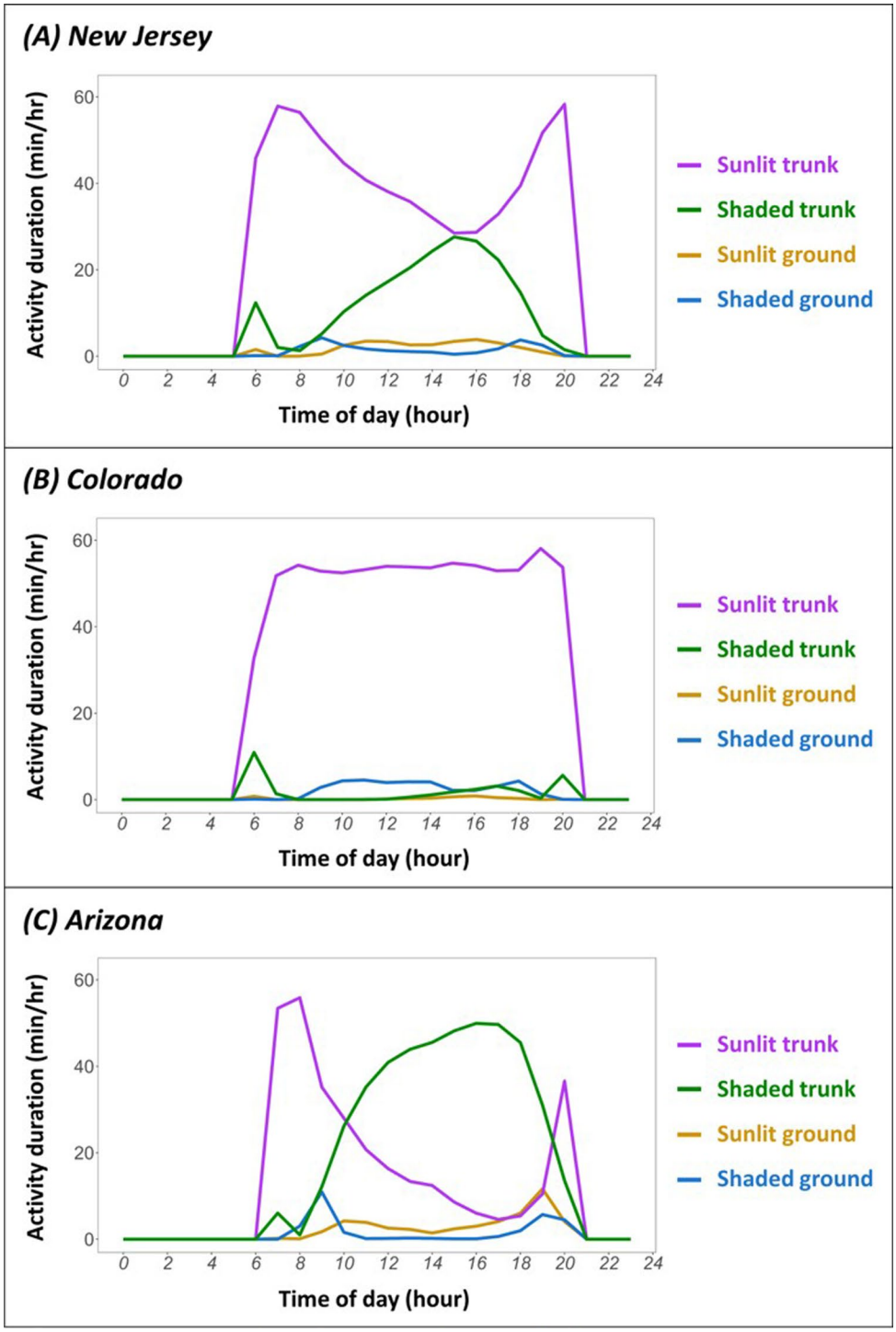

Extended Data Fig. 3 | A typical summer day for a simulated lizard. During mornings and evenings, lizards primarily used sunlit tree trunks, while shaded tree trunks were favoured during midday. The plots depict the lizard's predicted thermoregulatory behaviour in three different climates: (**a**) New Jersey, with a seasonal climate; (**b**) Colorado, with a cool climate; and (**c**) Arizona, with a warm climate. In Colorado's cool climate, lizards predominantly used sunlit tree trunks throughout the day. The values represent the average time spent in each micro-environment per hour, aggregated across all summer days (June-August) from 1980 to 2000.

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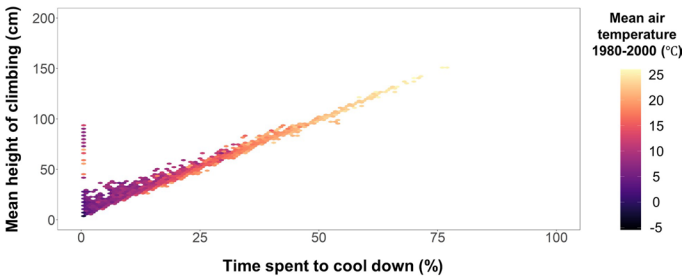

Extended Data Fig. 4 | Climbing height and the thermal benefit for lizards. Lizards climb higher when they need to cool down and lower when they need to warm up. The represented data considers only 'necessary climbing', which occurs when lizards must climb to maintain their body temperature within the desired activity range. The colour of each hexagon represents the average air temperature of locations sharing the same x and y values.

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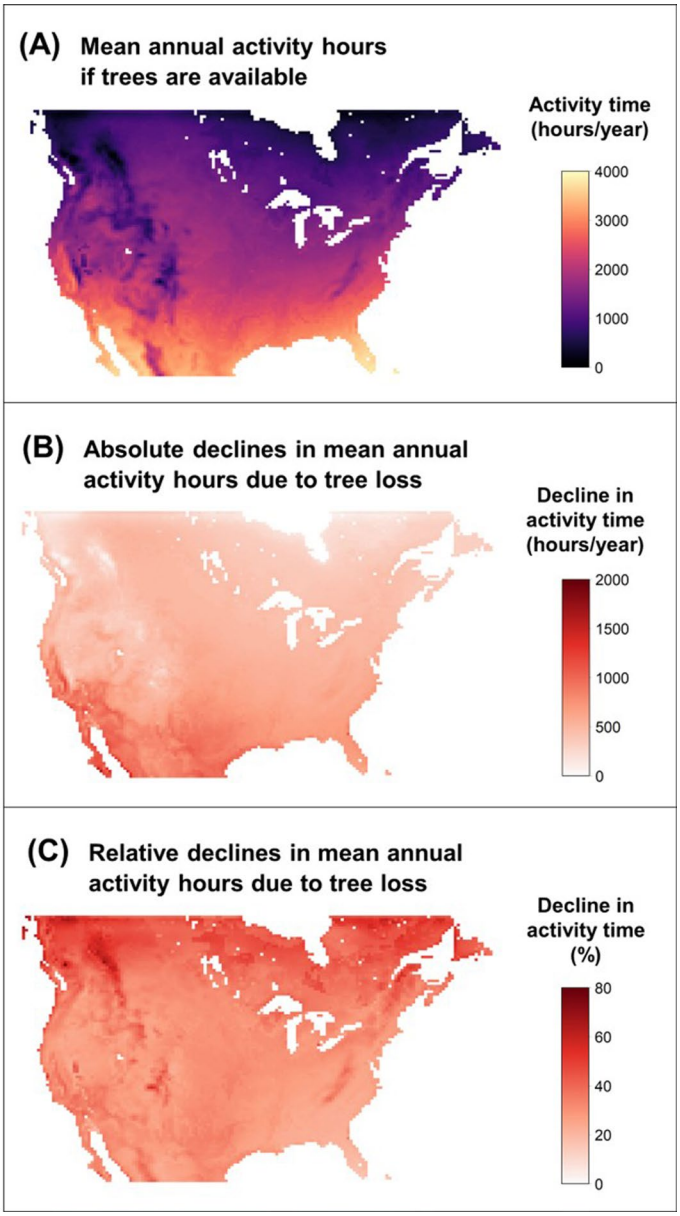

Extended Data Fig. 5 | The effect of tree loss on the annual activity time of lizards. Across the climatic gradient, tree loss is projected to significantly reduce lizards' activity time. Cooler locations are expected to show a greater relative reduction, while warmer locations may experience a more substantial absolute reduction. The panels illustrate: (**a**) Mean annual activity hours from 1980 to 2000 when lizards are able to climb trees; (**b**) Mean absolute decrease in annual activity hours from 1980 to 2000 due to tree loss; and (**c**) Mean relative decrease in annual activity hours attributable to tree loss. Mean annual activity hours were calculated by summing all active time units over the 20-year period, then dividing by 60 (to convert minutes to hours) and by 20 to determine the average yearly activity.

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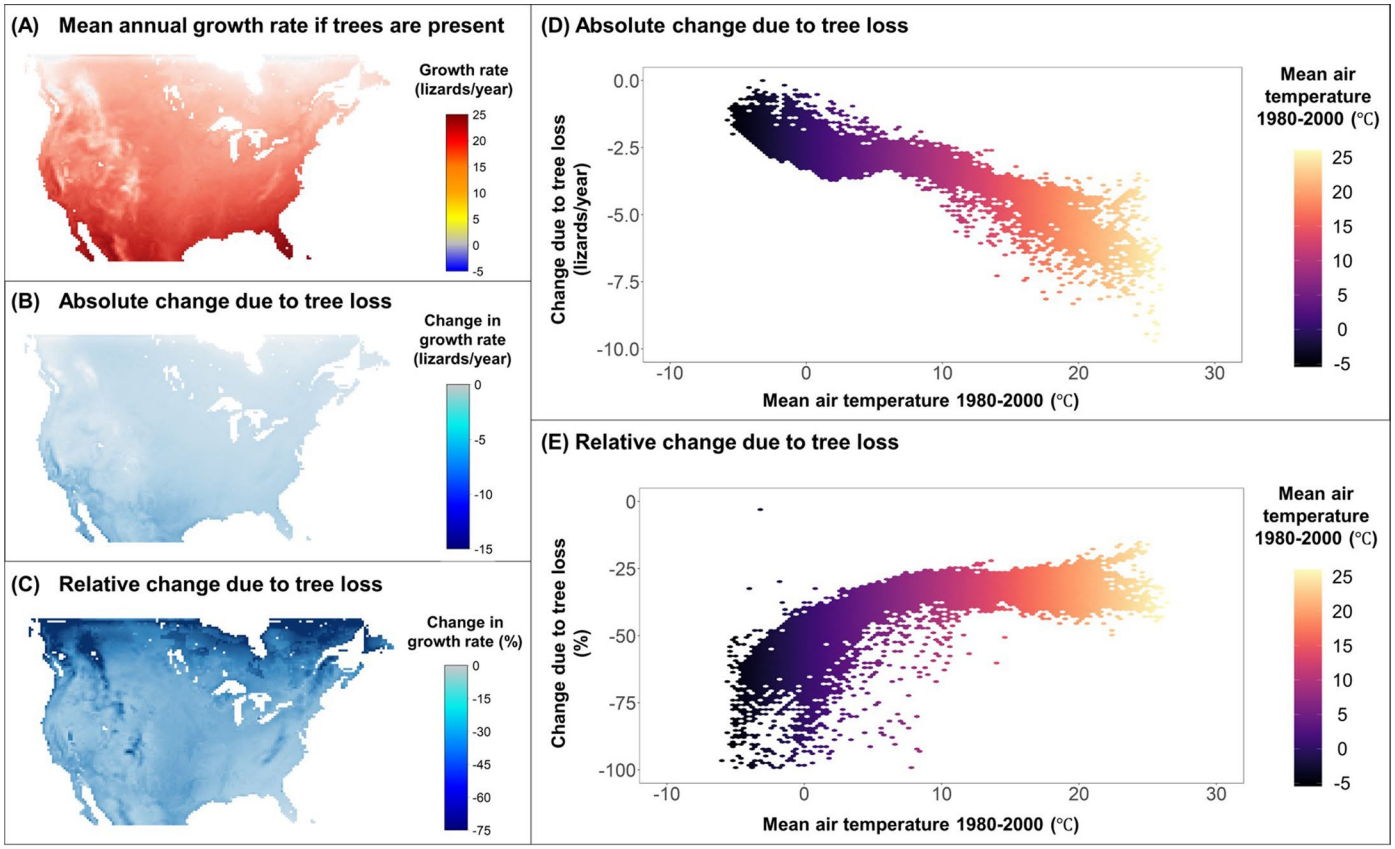

Extended Data Fig. 6 | The effect of tree loss on the annual growth rate of lizard populations. Tree loss is expected to reduce the annual growth rate of lizard populations across the entire climatic gradient, with a greater absolute decrease in warmer locations and a more pronounced relative decrease in cooler ones. The presented maps depict: (**a**) the mean annual growth rate when trees are available (no tree loss), (**b**) the absolute changes in mean annual growth rate (lizards/year) resulting from tree loss, and (**c**) the relative change in mean annual growth rate (%) due to tree loss. Additionally, we illustrate the correlation between climatic conditions and the (**d**) absolute (lizards/year) and (**e**) relative (%) changes in mean annual growth rate attributable to tree loss. The patterns revealed by the absolute and relative changes demonstrate opposite trends: while the absolute decrease in annual growth rate is more significant in warmer locations, the relative reduction is more substantial in cooler locations. In maps (D) and (E), the colour of each hexagon indicates the average air temperature of locations sharing the same x and y values.

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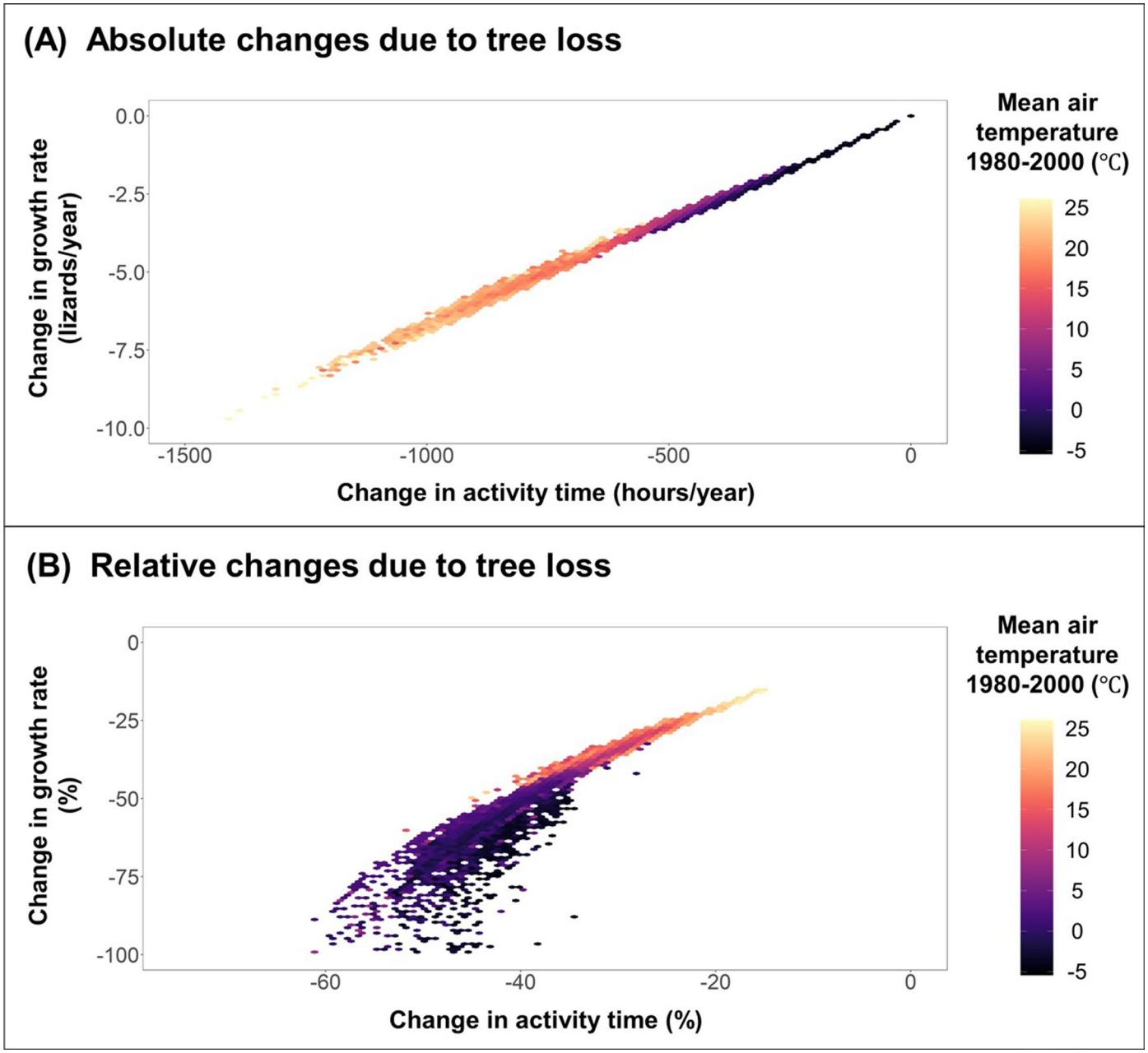

Extended Data Fig. 7 | The cascading effect of tree loss on activity times and populations' growth rates. Tree loss negatively impacts lizard activity time, leading to declines in population growth rates. In both aspects, warmer locations are predicted to experience a greater absolute reduction, whereas cooler locations will face a more significant relative reduction. The plots illustrate the correlation between tree loss and its effects on (**a**) Absolute changes (lizards/year and hours/year, for growth rates and activity times, respectively) and (**b**) Relative changes (%). The colour of each hexagon indicates the average air temperature of locations with the same x and y coordinates.

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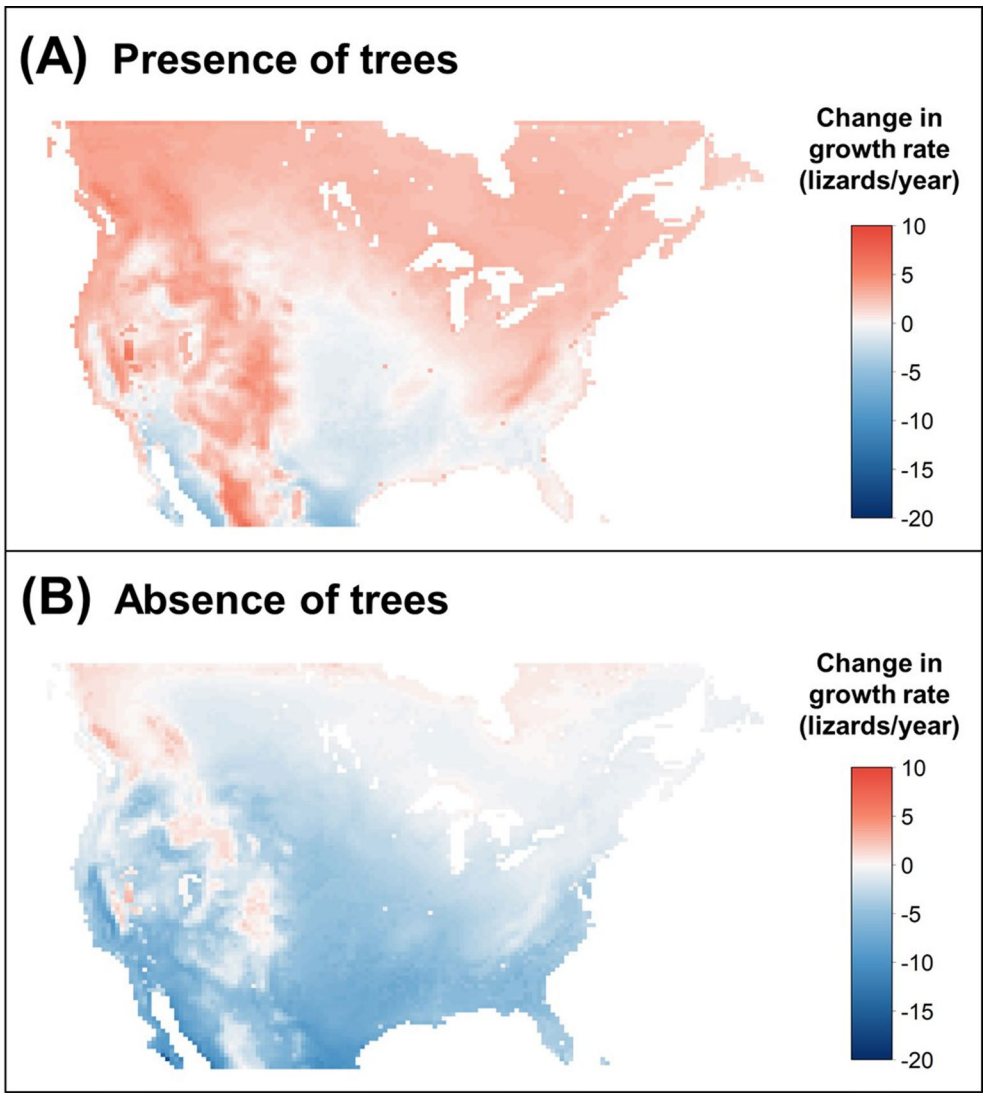

Extended Data Fig. 8 | Mapping the damaging effect of tree loss under climate change. The absence of trees is projected to cause most lizard populations to decline, counteracting any potential benefits from climate change. This includes populations currently anticipated to benefit from such changes. The maps illustrate the predicted impact of climate change on lizard mean annual population growth rates, comparing scenarios where (**a**) trees are available to those where (**b**) trees are absent due to deforestation.

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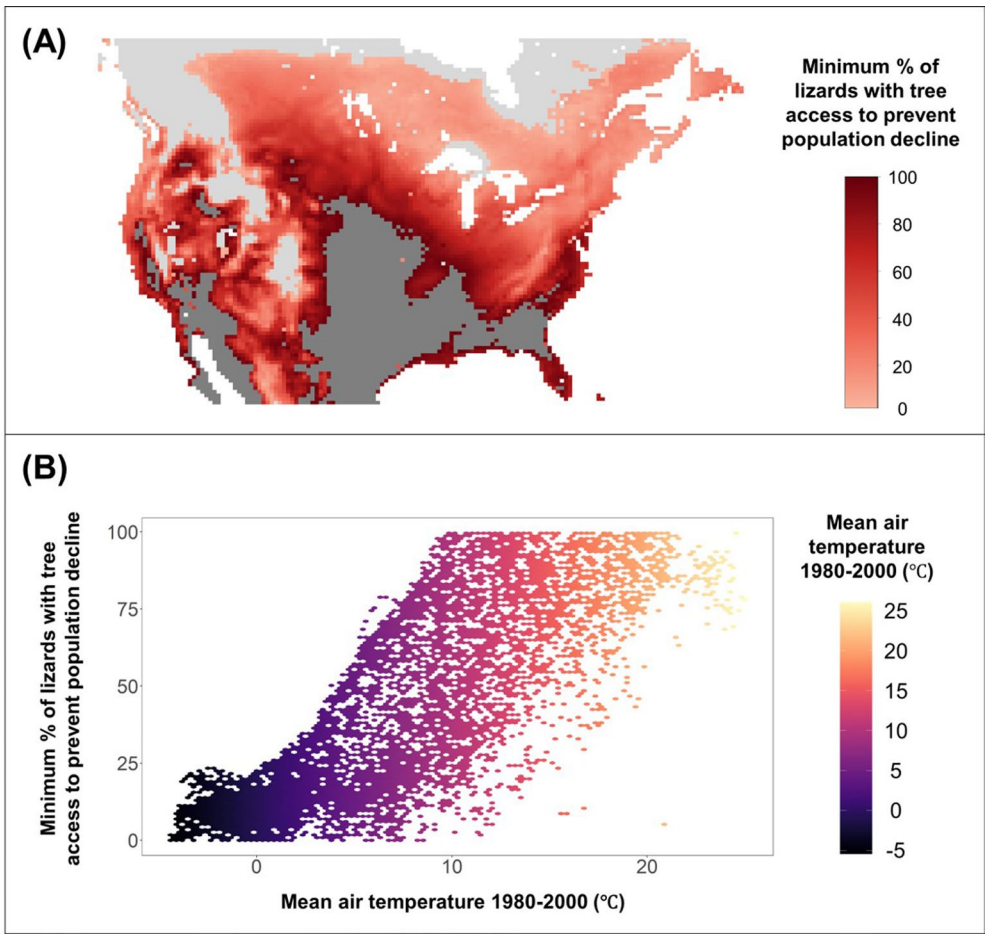

Extended Data Fig. 9 | Minimal tree availability needed to prevent population declines under climate change. We calculated the minimum proportion of the lizard population requiring access to trees to maintain a stable growth rate under climate change for each location (refer to Equation. 28). In (**a**) the map displays the minimum percentage of the lizard population needing tree access to avert decline. Grey shades represent areas where deforestation does not alter the impact of climate change: light grey signifies locations with population increases, and dark grey indicates declines, irrespective of deforestation. In (**b**), we demonstrate the correlation between these predictions and the mean temperature of each location, with each hexagon's colour denoting the average air temperature for areas with corresponding x and y coordinates.