PLOS CLIMATE

RESEARCH ARTICLE

Population distribution within the human climate niche

Barry A. Klinger[1]*, **Sadie J. Ryan**[2]

1 Department of Atmospheric, Oceanic, and Earth Sciences, George Mason University, Fairfax, Virginia, United States of America, **2** Department of Geography and the Emerging Pathogens Institute, University of Florida, Gainesville, Florida, United States of America

* bklinger@gmu.edu

Abstract

Climate change may pose an acute threat to humanity due to physical and biological constraints on regional habitability. A recent study proposed that the human climate niche is a narrow segment of the Earth's temperature range, with a mode of habitation around 13˚C. Here, the human climate niche is recharacterized using a novel graphical technique, the size-intensity chart. Several measures of population distribution were compiled to test the idea that humans live preferentially in the temperate range (10–20˚C) rather than the warm range (20–30˚C). The temperate range has a higher average population density (people/km^2), which suggests that it is more suitable for humans than the warm range. However, other population measures suggest the opposite. The warm range has a greater overall population; and regions with high population densities cover a greater land area and are home to more people in the warm range. Population density also depends on annual precipitation R; size intensity charts show that population density increases sharply with precipitation for $40 < R < 80$ cm/yr. The warm temperature range has a greater surface area with desert conditions of $R < 10$ cm/yr, but sparse habitation in dry regions does not explain the lower average population density of the warm range. Overall, human habitation patterns do not show a consistent preference for temperate over warm lands, and that precipitation may mediate, but not limit this relationship.

Check for updates

Citation: Klinger BA, Ryan SJ (2022) Population distribution within the human climate niche. PLOS Clim 1(11): e0000086. https://doi.org/10.1371/journal.pclm.0000086

Editor: Samuel Nii Ardey Codjoe, University of Ghana, GHANA

Received: June 3, 2022

Accepted: October 10, 2022

Published: November 9, 2022

Data Availability Statement: Zenodo repository: https://doi.org/10.5281/zenodo.5750670.

Funding: The authors received no specific funding for this work.

Competing interests: The authors have declared that no competing interests exist.

1 Introduction

Climate change and population growth [1, 2] raise the question of the sustainability of future human population distributions. One lens through which to view this question is the ecological concept of a climate 'niche', the optimally suitable combination of conditions in which an organism can satisfy the basics of feeding and reproducing [3–6]. To what extent are current and past population distributions constrained by such a niche?

In recent work [7], suggest that humans occupy a "narrow part of the climate envelope available on the globe, characterized by a major mode around ~11˚C to 15˚C" annual mean temperature T. The mode they refer to is based on tabulating the population and land area falling within various temperature intervals and plotting population density D (people/km^2) as a function of temperature. The mode itself is a local maximum in $D(T)$. They contrast this temperate mode with a projected future in which large populations are threatened by unprecedented temperatures greater than 29˚C [7]. While these statements are true, they may give a misleading impression of just how narrow the human climate niche is. Their plot of $D(T)$ (their Fig 2) shows an additional warm local maximum around 23–28˚C. The warm mode has a peak population density about half of the temperate one, which [7] interpret as implying reduced suitability for humans. Are annual mean temperatures in the 20's Celsius really less suitable for human habitation than temperatures in the teens? Do moderate temperatures intrinsically support higher densities of humanity, or are they an accident of history?

Xu et al. [7], building on previous descriptive work [8], look at the distribution of people and agriculture over time. Human habitation is concentrated at low altitudes, near coasts, and near fresh-water bodies [8–10]. A "suitability" index that includes topography, temperature, humidity, water resources, and vegetation and applied to China shows greatest suitability in southeast China [11] but also shows significant variation between this measure and actual population density [12]. Several studies have looked at human migration and its relation to climate during the original radiation of humans from Africa [13–15], and during prehistory [16–20], but technological innovations may have made human populations less sensitive to environmental conditions than they were during prehistory. For instance, while suitability for agriculture may be a key prerequisite for maintaining high population densities, in recent generations population centers and agricultural centers are growing increasingly decoupled [9, 21]. Other papers have looked at the role of interannual-to-decadal climate change in instigating migration and civil conflict [22–26], but it is difficult to connect such episodes of population change to long-term population trends.

Here, we take a second look at observations of population distributions to help answer the questions posed above rather than investigating the mechanisms of population distribution. First, we consider how the actual population, as opposed to population density, depends on temperature. Clearly, large numbers of people live in the tropics, but how many live in different temperature ranges? While high population density in a given temperature range suggests high suitability for that temperature range, high population in a different temperature range may also suggest high suitability.

Tabulating either population or population density as a function of temperature involves aggregating population distributions from all over the world. However, human population densities are notoriously heterogeneous. The population density in a given temperature range is a combination of highly crowded cities, sparsely-populated rural areas, and every density inbetween. Thus the lower global population density of temperatures in the 20s ˚C (compared to the 10s) obscures a wide range of local population density patterns. For most temperatures, the question of whether any people live at various population densities at that temperature misses the broader point; generally some do. The question is how many live at each population density. We are not aware of any study to date quantifying the joint distribution of population with temperature and population density. If a large number of people in warm regions live in high-density locations, this also suggests that warm regions may be more suitable for humans than the average population density for those temperatures would indicate.

Finally, another important climate parameter for human habitation is annual mean precipitation, here denoted R. Deserts have low human population density, but at what precipitation value does population density begin to increase, and what is the shape of the distribution of population density with R? Moreover, if deserts tend to be hot, then it is possible that the lower population density of warmer regions is really due to a lack of water rather than an excess of heat? By controlling the temperature distribution of population for precipitation, we can test this question.

We illustrate the distributions discussed above with size-intensity plots, a novel technique for simultaneously displaying "per area" and "total" quantities. This kind of graph, described in more detail in Section 2 below, is well suited to the questions posed here, but also has wide applicability to geographic, social, and demographic data.

2 Materials and methods

Data were derived from data sets cited in [7]. Mean annual temperature, T and annual mean precipitation, R are derived from data from WorldClim version 2.1 [27] "bioclimatic variables" averaged over 1970–2000 (10-minute resolution). The same climate data was used for both years (2000 and 1800) of population data. While Fig 1 only displays 50˚S to 60˚N, subsequent analysis was based on fields between 60˚S and 80˚N. This excludes Antarctica; Greenland, which is also largely covered by ice sheets and has a small population ($<$ 100,000), is also excluded from calculations.

Population data for 2000 CE and 1800 CE were obtained from the History Database of the Global Environment (HYDE, [28]). The original data grid had a resolution of 5 minutes; adjacent gridpoints were interpolated to the resolution of the WorldClim grid. Population density was derived by dividing population per gridpoint by area per gridpoint, both of which are included in HYDE data. The visualization technique in Figs 1 and 2 was firsit applied to 2015 population estimates from Gridded Population of the World data set (GPWv4, [29]) by interpolating climate data to GPWv4's 15-minute grid. The figures were nearly identical to those created using HYDE data, indicating that the results sensitive to the change in population data source.

We analyzed global population data by "binning it": selecting all the land grid cells of the HYDE data described above which meet a criteria such as falling within a certain temperature range. For instance, we divide the temperature range into ΔT = 2˚C bins, with the i^{th} bin

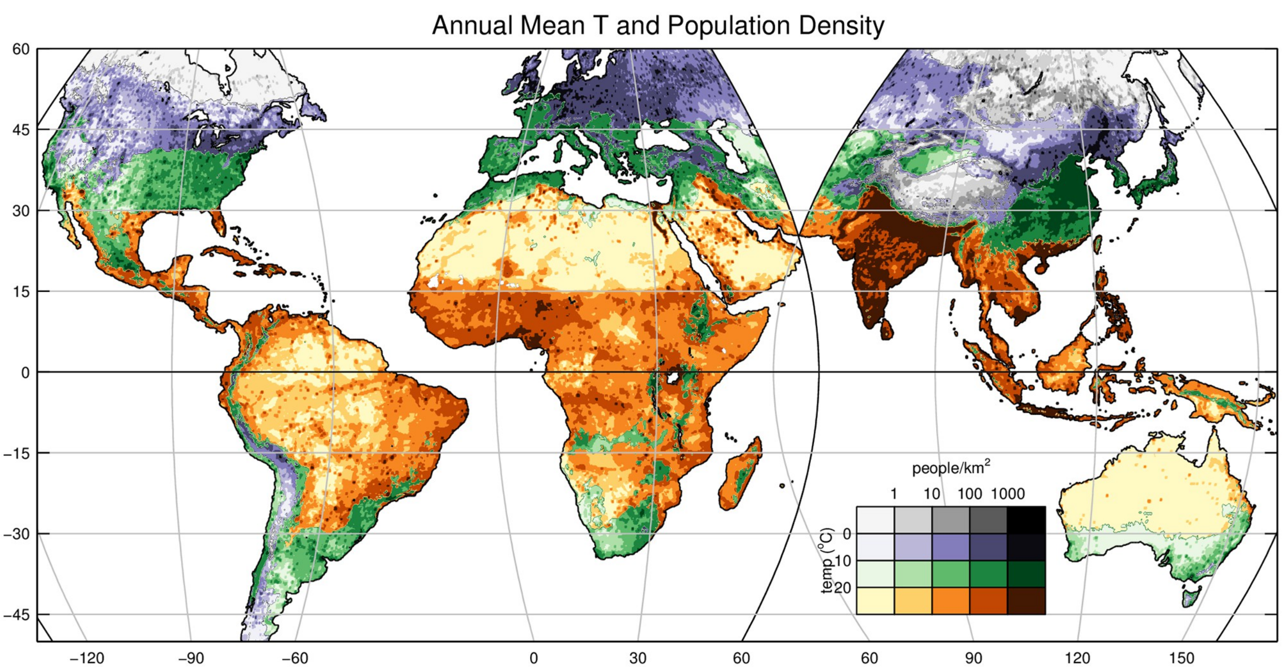

Fig 1. Annual mean land temperature in 10˚C contour intervals (hue), and population density separated by D_j = 1, 10, 100, 1000 people/km^2 (shade), mapped in separate equal-area (sinusoidal) projections for the Americas, western Eurasia/Africa, and eastern Asia/eastern Pacific.

https://doi.org/10.1371/journal.pclm.0000086.g001

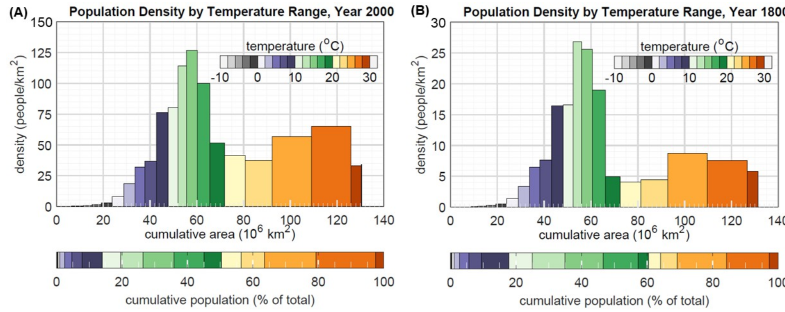

Fig 2. Rectangles representing population distributions in the year (A) 2000 CE and (B) 1800 CE. Each rectangle represents a 2˚C temperature range. The width, height, and area of each rectangle give A_i, D_i, and P_i, respectively, of the i^{th} temperature range. Rectangles are arranged from left to right in order of ascending temperature limits, and values of area marked on horizontal axis are cumulative. Bars below each chart represent population share of each temperature range.

https://doi.org/10.1371/journal.pclm.0000086.g002

defined by a lower limit T_i. The land area of all grid cells with $T_i \leq T < T_i + \Delta T$ is summed to form a land area A_i. The combined population of all the cells meeting this criteria is P_i. The population density for that temperature bin is $D_i = P_i/A_i$.

Similarly, we divided the precipitation range into bins of width ΔR so that the i^{th} bin consists of all grid cells with $R_i \leq R \leq R_i + \Delta R$. Unlike temperature, the precipitation bins are not of equal size; we choose ΔR = 10 cm/yr for $R < 80$ cm/yr, ΔR = 20 cm/yr for $80 \leq R < 160$ cm/yr, ΔR = 40 cm/yr for $160 \leq R < 320$ cm/yr, and ΔR = 160cm/yr for $320 \leq R < 960$ cm/yr. If the precipitation bins were of equal width, the area A_i of bins in the 80 to 320 cm/yr range would be much smaller than the bins for lower R. Even with the nonuniform ΔR, A_i decreases for $R_i > 240$ cm/yr.

To simultaneously compare area, population, and population density among different geographical units, we used a size-intensity chart. In the temperature example above, each temperature bin is represented by a rectangle of width proportional to the land area A_i and height proportional to the population density D_i. Since total population of land is $P_i = A_i D_i$, the area in the graph of each rectangle is proportional to P_i. Hence the graph can simultaneously show three variables at once.

It is worth commenting on the size-intensity chart, a simple but powerful technique for data visualization. It is currently rarely used even though it is potentially useful for displaying a wide range of information. There are many examples in economics, geography, and social science in which both the rate and total size are important. For instance, to compare national carbon emissions, it is relevant to know both the per capita emissions (height of a rectangle representing each country), national population (width of the rectangle), and total emissions (area of the rectangle). A snapshot of global economic activity can be represented with each rectangle representing per capita GDP, population, and total GDP with width, height, and area, respectively. To analyze the distribution of deaths from Covid-19 in the United States, the width, height, and area of each rectangle could represent deaths per capita, population, and total deaths for each state or region. In this paper, we make extensive use of this method of visual display of information.

In addition to simply using temperature bins to analyze population distributions, we also used temperature jointly with other variables. In these cases, we used a smaller number of temperature bins, with $\Delta T = 10$˚C. For each temperature bin with lower bound T_j, we separated land grid cells into precipitation bins R_i = 10, 40, 160, 960 cm/yr.

Since the average population density in a given temperature bin represents areas with a very wide range of population densities, we also use the 10˚C temperature bins and population density bins to aggregate the total area that falls within a given temperature and density range. For population density we have bins for $D < 1$ person/km^2, $1 \leq D < 10$ people/km^2, $10 \leq D < 100$ people/km^2, $100 \leq D < 1000$ people/km^2, and $D > 1000$ people/km^2. These ranges very roughly correspond to wilderness, sparsely populated rural areas, relatively dense rural areas, suburban, and urban areas, respectively. This allows us to compare area and population of a given density range between different temperature ranges.

All analyses were conducted in Matlab software written by the first author; it can be found in Github repository https://doi.org/10.5281/zenodo.5750670.

3 Results

A map in which annual mean land surface temperature T is divided into 10˚C intervals (Fig 1) shows a large warm (20–30˚C) band, with smaller areas in temperate (10–20˚C) and cool (0–10˚C) bands. Population density D, shown in the same map, spans a range of over 4 orders of magnitude. Large land areas have hardly any population ($D < 1$ people/km^2) and much of humanity lives in regions with $D > 100$ people/km^2. The warm band contains prominent large regions of high population densities in South Asia, Southern China, Nigeria, and elsewhere. This qualitative impression suggests that the population density could be as high in the warm band as in the temperate band.

How does total population of the warm mode compare to the total for the temperate mode? To answer this question, we divide the temperature range into $\Delta T = 2$˚C bins, and plot the resulting area A_i, population density D_i, and population P_i for each temperature bin with a size-intensity chart (Fig 2A). **Sec. 2** describes the binning process and the rationale for size-intensity charts.

The size-intensity chart reproduces the temperate and warm modes shown by [7], but also quantifies the large land area of the warm temperature range. Half of the human population lives in the warm range. This can be seen both in the area of the orange/brown rectangles compared to the green rectangles, and more clearly by the plot of cumulative population in bottom of the figure. About 1.6 billion people live at 12–18˚C compared to about 2.2 billion at 24–28˚C. The temperate mode has the greatest population density, but the warm mode has the greatest population. The distribution of population with temperature is by no means constant through time. The warm mode is more prominent in 2000 than it was in 1800 (Fig 2B), with its population share growing from about 40% of humanity in 1800 to 50% in 2000.

What is the significance of the higher population density at 15˚C? It is important to remember that the population densities shown in Fig 2 are calculated from very wide distributions of D (Fig 1). As discussed in **Sec. 2**, adding up the land area in different population density ranges for each 10˚C temperature range illustrates how well different population densities are represented by a given temperature range. Fig 1 shows which regions on Earth have population densities in various ranges (see text above). In Fig 3, for each of 5 temperature ranges, we display the area of land within each of the population density ranges. The warm band collectively contains more territory of both $100 < D < 1000$ people/km^2 and $D > 1000$ people/km^2 than the temperate band (Fig 3A). Thus, the greater average population density of the temperate range obscures the fact that high-density human populations occur in larger areas of the warm range.

The total population numbers (printed on the graph in Fig 3A) also show a warm-range bias. The highest density class ($D > 1000$ people/km^2) has nearly 700 million people in the temperate temperature range, and nearly a billion in the warm range. There is a similar

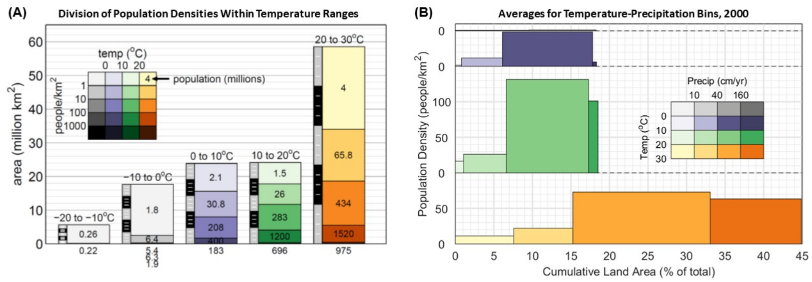

Fig 3. (A) Area of Earth's surface (excluding Antarctica and Greenland) within given temperature and population density ranges. Colors correspond to those in same *T*-*D* range in Fig 1. Numbers represent population in millions within each area (below stack for small-area rectangles at bottom of stack). (B) As in Fig 2, but with each rectangle representing regions within a given range of temperature and precipitation. Hue of each represents temperatures as in Fig 1, but shade represents precipitation ranges. Each row of rectangles represents a given temperature interval, arranged in order of ascending precipitation categories; characteristics of regions represented by a given rectangle are independent of the rectangle's location.

https://doi.org/10.1371/journal.pclm.0000086.g003

discrepancy in the next density class ($100 < D < 1000$ people/km^2), 1200 million and 1500 million in temperate and warm ranges, respectively. For each of the two greatest population density ranges, both the area and total population is greater for the warm range than for the temperate range.

Still, settlement with $D > 100$ people/km^2 takes up almost twice as big a fraction of temperate regions than warm ones: about 18% versus 10% of total land area (Fig 3A). Is this an indication of greater suitability of temperatures in the 10–20˚C range?

The warm temperature band has vast expanses of sparse population ($D < 1$ people/km^2) in desert regions (*e.g.* Sahara and the Australian Outback) and in the Amazon rainforest. Additional low-population areas ($10 < D < 1$ people/km^2) fill much of the Arabian Peninsula, the fringes of the Sahara and Kalahari deserts, and jungles in Central Africa and elsewhere (Fig 1). The temperate band contains relatively small sparsely-populated dry zones, such as the Taklimakan Desert north of the Himalayas, and southern Africa. The sparsely populated area comprises 40% of the warm band but only about 26% of the temperate band (Fig 3A). This points to the question of whether the warm band has a lower population density because it has large deserts.

We tested this question by dividing the land territory of the Earth into 10˚C temperature intervals and dividing the intervals into different levels of precipitation *R*, including desert ($R < 10$ cm/yr), dry ($10 \leq R < 40$ cm/yr), moderate ($40 \leq R < 160$ cm/yr) and wet ($R \geq 160$ cm/yr). A size-intensity plot shows the area and population of each bin in (T, R) space (Fig 3B). As expected, desert-level rainfall is associated with very low population density in all temperature ranges. Additionally, deserts take up a larger fraction of the warm band area (about 1/6th) than of the temperate band (about 1/18th). However, looking only at moderate-rainfall regions, the temperate band still has twice the population density of the warm band. Lower population density in the warm band is not due to greater extent of dry, sparsely-populated land.

The population distribution as a function of *R* alone shows a maximum population density of nearly 100 people/km^2 at 120–140 cm/year (Fig 4; see also [30], for a more traditional histogram). Average population density for desert and dry regions is about 1/6 of the peak population density, with relatively little variation. It is surprising that desert regions with extremely low precipitation do not have much lower population density than dry regions (10–40 cm/yr). In part, this is due to large areas of very cold (-10˚C $< T <$ 0˚C) dry land with miniscule population densities (Fig 3). Another reason is that some low-*R*, high-*P* regions are fed by rivers

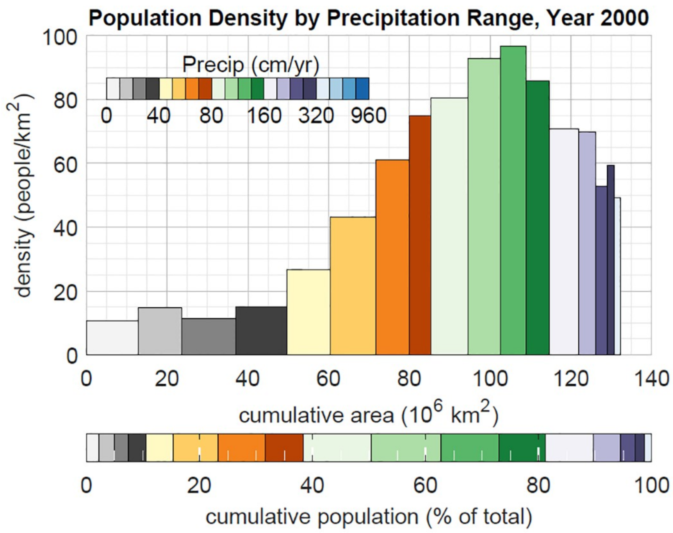

Fig 4. Like Fig 2 but with each rectangle representing a range of annual average precipitation *R* for the year 2000 CE. Precipitation ranges are 10 cm/year for $R < 80$ cm/year, 20 cm/year for $80 \leq R < 160$, 40 cm/year for $160 \leq R < 320$, and 160 cm/yr for $320 \leq R < 960$.

https://doi.org/10.1371/journal.pclm.0000086.g004

carrying water from wetter environments. The effect is so dramatic that it can be seen in the population map (Fig 1), with hundreds of millions living along the Nile River, Indus, and Tigris-Euphrates rivers. At the other extreme, wet areas have somewhat lower population density than the peak value, but still much higher than the dry regions.

4 Discussion and conclusion

Extremely cold regions seem to be beyond the human climate niche: less than 1% of humanity lives below 0˚C, an area that covers almost 20% of the total land (excluding Antarctica and Greenland). Large populations live at virtually all annual-mean temperatures from 0˚C to 30˚C, including those close to the maximum. Similarly, humans occupy almost the entire range of annual precipitation, but with much sparser habitation in regions with less than an average of 40 cm/year.

While extremely low population density *D* indicates genuine barriers to habitation such as difficulty growing food, it is harder to interpret the smaller average population density of the warm (20–30˚C) band compared to the temperate (10–20˚C) band. Xu et al. [7] took this measurement as a sign that the temperate band was more suitable for human habitation than the warm band. In this paper, we tested some alternate measures of how populated the warm and temperate bands have been recently.

Looking at overall population, we see that the warm band had more people than the temperate band, in part because more of the Earth's land surface falls in the warm band. Next, we disaggregated population density by dividing humanity into different ranges of population density. Hundreds of millions of people can and do live at high densities in warm climates. In fact, for the most crowded parts of the Earth (density classes 100–1000 people/km^2 and >1000 people/km^2) more people and more land are in the warm band then in the temperate. This strongly signals that habitable spaces are not contrained to temperate bands.

Since precipitation strongly influences human populations due to the demand for water, we also examined population density as a function of annual precipitation *R*. Population density sharply increases with *R* from 40 to 80 cm/yr. Interestingly, the lowest precipitation rates ($R<$

10 cm/yr) do not have much lower population density than regions with $10 < R < 40$ cm/yr. Part of the reason is that the transport of water to some ultra-low precipitation regions by large rivers increases the population density that can live there, and that the inclusion of some very cold regions lowered the population density of the 10–40 cm/yr regions.

We hypothesized that the lower population density in the warm band is due to deserts covering a higher fraction of the warm band's land area. While the warm band has a higher fraction of desert, when we controlled for rainfall, we still found population density to be higher in temperate regions. There are many additional factors that may contribute to these density differences, including human factors such as technology and economics, climate factors such as seasonal variations, and other factors such as topography and soil quality. We hope that future research can explore how and where these types of factors play into the constraints on the human climate niche.

In conclusion, human habitation patterns do not give a clear indication of whether warm or temperate temperature bands are more suitabile for humans. As noted by [7], population densities are, on average, higher in the temperate band. This is true even if we control for precipitation, and exclude deserts from the comparison. This finding would indicate that the temperate band is more suitable. Yet the warm band has a larger human population, a larger land area and higher population in regions of high population density. In addition, the ratio of warm to temperate population densities have also changed significantly over time. All these findings argue against higher suitability for the temperate range, and suggest that the human climate niche may be broader and warmer.

The niche concept in this context may suffer from a couple of limitations. One assumption is ideal free distribution (IFD): organisms on the landscape have access to all of that landscape, in order to choose to be in an optimal niche space. It also assumed that at the center of the niche has higher density of individuals, because it is optimal [31]. While we can perhaps assume a degree of IFD on the macroscale (the entire globe), if climate is the limiting factor, we may see lagged responses at the scale of population density movement. Additionally, there are assumptions of population stability or stationarity baked into these concepts, which may be inappropriate in a world that is changing as rapidly as ours. Indeed, invasive species may represent a good analogy for niche-shifts when moving to new ranges [32–34].

Anthropogenic climate change will change T for many people to ranges hotter than ever experienced in recorded history. For many other people, the temperature change will merely be from one livable temperature to a warmer, but still livable, one. None of this study's findings negate the profound risks posed by anthropogenic climate change [35]. The large decrease in population density from the 26–28˚C range to the 28–30˚C range is consistent with the concept that temperatures above 30˚C are significantly less suitable for humans. Even if half the population already lives at $T > 20$˚C, "moving" some of them to conditions outside the range of any prior human experience will bring physiological harm, crop failure, and ecological damage. While global heating may make some cold lands more habitable, physically moving people to take advantage of improving temperatures may not be feasible. Finally, concurrent and co-located climate-change-driven phenomena, such as rising sea levels and extreme events, are separate from the direct effects of local temperature, but must not be overlooked as compounded risks to the future of the human niche on this planet.

Author Contributions

Conceptualization: Barry A. Klinger, Sadie J. Ryan.

Data curation: Barry A. Klinger.

Formal analysis: Barry A. Klinger.

Investigation: Barry A. Klinger.

Methodology: Barry A. Klinger.

Project administration: Barry A. Klinger.

Software: Barry A. Klinger.

Supervision: Barry A. Klinger.

Validation: Barry A. Klinger.

Visualization: Barry A. Klinger.

Writing – original draft: Barry A. Klinger, Sadie J. Ryan.

Writing – review & editing: Barry A. Klinger, Sadie J. Ryan.

References

1. Riahi K, van Vuuren DP, Kriegler E, Edmonds J, O'Neill BC, Fujimori S, et al. The Shared Socioeconomic Pathways and their energy, land use, and greenhouse gas emissions implications: An overview, Glob Environ Change. 2017; 42: 153–168.
2. O'Neill BC, Kriegler E, Ebi KL, Kemp-Benedict E, Riahi K, Rothman DS, et al. The roads ahead: Narratives for shared socioeconomic pathways describing world futures in the 21st century. Glob Environ Change. 2017; 42, 169–180.
3. Grinnell J. The Niche-Relationships of the California Thrasher. The Auk. 1917; 34: 427–433. https://doi.org/10.2307/4072271
4. Vandermeer JH. Niche Theory, Ann Rev Ecol Syst. 1972; 3: 107–132, https://doi.org/10.1146/annurev.es.03.110172.000543
5. Hutchinson GE. Concluding Remarks. Cold Spring Harbor Symp Quant Biol. 1957; 22: 415–427
6. MacArthur R. Population Ecology of Some Warblers of Northeastern Coniferous Forests. Ecology. 1958; 39: 599–619, https://doi.org/10.2307/1931600
7. Xu C, Kohler TA, Lenton TM, Svenning J-C, Scheffer M. Future of the human climate niche, Proc Nat Acad Sci. 2020; 117: 11350–11355. https://doi.org/10.1073/pnas.1910114117 PMID: 32366654
8. Small C, Cohen J. Continental physiography, climate, and the global distribution of human population. Curr Anthropol. 2004; 45: 269–277.
9. Kummu M, de Moel H, Salvucci G, Viviroli D, Ward PJ, Varis O. Over the hills and further away from coast: global geospatial patterns of human and environment over the 20th-21st centuries, Environ Res Lett. 2016; 11: https://doi.org/10.1088/1748-9326/11/3/034010
10. Xiao CW, Feng ZM, Li P, You Z, Teng JK. Evaluating the suitability of different terrains for sustaining human settlements according to the local elevation range in China using the ASTER GDEM, J Mountain Sci. 2018; 15: https://doi.org/10.1007/s11629-018-5058-3
11. Feng Z, Yang Y, Zhang D, Tang Y. Natural environment suitability for human settlements in China based on GIS, J Geogr Sci. 2009; 19: 437–446.
12. Feng Z, Yang Y, You Z, and Zhao Y. A GIS-based study on sustainable human settlements functional division in China, J Resour. Ecol. 2010; 1: 331–338.
13. deMenocal PB, Stringer C. Human migration: Climate and the peopling of the world. Nature. 2016; 538: 49–50. https://doi.org/10.1038/nature19471 PMID: 27654915
14. Timmermann A, Friedrich T. Late Pleistocene climate drivers of early human migration. Nature. 2016; 538: 92–95. https://doi.org/10.1038/nature19365 PMID: 27654920
15. Gavashelishvili A, Tarkhnishvili D. Biomes and human distribution during the laste ice age, Global Ecol Biogeogr. 2016; 25: 563–574.
16. D'Andrea WJ, Huang Y, Fritz SC, Anderson NJ. Abrupt Holocene climate change as an important factor for human migration in West Greenland. Proc Natl Acad Sci U S A. 2011; 108: 9765–9769. https://doi.org/10.1073/pnas.1101708108 PMID: 21628586
17. Cordell LS, Van West CR, Dean JS, Muenchrath DA. Mesa Verde settlement history and relocation: Climate change, social networks, and Ancestral Pueblo migration. Kiva. 2007; 72: 379–405.

18. Manning K, Timpson A. The demographic response to Holocene climate change in the Sahara, Quat Sci Rev. 2014; 101: 28–35.
19. Tyson PD, Lee-Thorp J, Holmgren K, Thackeray JF. Changing gradients of climate change in southern Africa during the past millennium: implications for population movements, Climatic Change. 2002; 52: 129–135.
20. Dillehay TD. Climate and human migrations. Science. 2002; 298: 764–765.
21. Zhang YJ, Zhao J, Yan YX, Shi Y, Yu Q. Relationship of population migration, crop production pattern, and socioeconomic development: evidence from the early 21st century, Environ Res Lett. 2021; 16: 074045.
22. Abel GJ, Brottrager J, Cuaresma JC, Muttarak R. Climate, conflict and forced migration. Glob. Environ Change. 2019; 54; 239–249.
23. McLeman R. Thresholds in climate migration. Popul Environ. 2018; 39; 319–338.
24. Chort I, de la Rupelle M. Determinants of Mexico-US outward and return migration flows: a state-level panel data analysis. Demography. 2016; 53: 1453–1476.
25. Mueller V, Gray C, Kosec K. Heat stress increases long-term human migration in rural Pakistan. Nat Clim Chang. 2014; 4: 182–185. https://doi.org/10.1038/nclimate2103 PMID: 25132865
26. Reuveny R. Climate change-induced migration and violent conflict. Polit Geogr. 2007; 26: 656–673.
27. Fick SE, Hijmans RJ. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas, Int J Climatol. 2017; 37: 4302–4315, https://doi.org/10.1002/joc.5086
28. Klein Goldewijk K, Beusen A, Doelman J, Stehfest E. Anthropogenic land use estimates for the Holocene; HYDE 3.2. Earth System Science Data. 2017; 9: 927–953.
29. Doxsey-Whitfield E, MacManus K, Adamo SB, Pistolesi L, Squires J, Borkovska O, et al. Taking advantage of the improved availability of census data: a first look at the gridded population of the world, Version 4, Pap Appl Geogr. 2015; 1: 226–234, https://doi.org/10.1080/23754931.2015.1014272
30. Oki T, Quiocho RE. Economically challenged and water scarce: identification of global populations most vulnerable to water crises. Int J Water Resour Dev. 2020. https://doi.org/10.1080/07900627.2019.1698413
31. Martínez-Meyer E, Díaz-Porras D, Peterson AT, Yáñez-Arenas C. Ecological niche structure and rangewide abundance patterns of species. Biol Lett. 2014; 23: 1356–1365.
32. Pili AN, Tingley R, Sy EY, Diesmos MLL, Diesmos AC. Niche shifts and environmental non-equilibrium undermine the usefulness of ecological niche models for invasion risk assessments. Sci Rep. 2020; 10: 7972. https://doi.org/10.1038/s41598-020-64568-2 PMID: 32409706
33. Early R, Sax DF. Climatic niche shifts between species' native and naturalized ranges raise concern for ecological forecasts during invasions and climate change. Glob Ecol Biogeogr. 2014; 23: 1356–1365.
34. Gallien L, Douzet R, Pratte S, Zimmermann NE, Thuiller W. Invasive species distribution models—how violating the equilibrium assumption can create new insights, Glob Ecol Biogeogr. 2012; 21: 1126–1136.
35. Field CB, Barros VR, Mach KJ, Mastrandrea MD, van Aalst M, Adger WN, et al. Technical summary. In: Field CB, Barros VR, Dokken DJ, Mach KJ, Mastrandrea MD, Bilir TE, et al, editors. Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, United Kingdom and New York, USA: Cambridge University Press; 2014; pp. 35–94.