Achieving climate connectivity in a fragmented landscape

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The contiguous United States contains a disconnected patchwork of natural lands. This fragmentation by human activities limits species’ ability to track suitable climates as they rapidly shift. However, most models that project species movement needs have not examined where fragmentation will limit those movements. Here, we quantify climate connectivity, the capacity of landscape configuration to allow species movement in the face of dynamically shifting climate. Using this metric, we assess to what extent habitat fragmentation will limit species movements in response to climate change. We then evaluate how creating corridors to promote climate connectivity could potentially mitigate these restrictions, and we assess where strategies to increase connectivity will be most beneficial. By analyzing fragmentation patterns across the contiguous United States, we demonstrate that only 41% of natural land area retains enough connectivity to allow plants and animals to maintain climatic parity as the climate warms. In the eastern United States, less than 2% of natural area is sufficiently connected. Introducing corridors to facilitate movement through human-dominated regions increases the percentage of climatically connected natural area to 65%, with the most impactful gains in low-elevation regions, particularly in the southeastern United States. These climate connectivity analyses allow ecologists and conservation practitioners to determine the most effective regions for increasing connectivity. More importantly, our findings demonstrate that increasing climate connectivity is critical for allowing species to track rapidly changing climates, reconfiguring habitats to promote access to suitable climates.

As the climate continues to change throughout the 21st century, many species will be stressed by increasingly extreme climates (1) and forced to adjust through either behavioral or phenotypic plasticity, through rapid evolutionary adaptation, or by moving to more climatically suitable areas. Species have already begun shifting their distributions in response to changing climates, generally poleward and upward in elevation (2–4). However, the United States is fragmented by human infrastructure, such as urbanization, roads, and farms. This disconnected patchwork of natural lands limits the ability of species to reach newly suitable regions, even if such areas exist (5–7). Movement barriers have already resulted in some extirpations, demonstrating the fragility of populations that cannot access climatically suitable habitats (8, 9). However, we lack a way to describe, quantify, and assess how these interacting climate and anthropogenic dynamics affect species’ ability to move on the landscape.

Here, we quantify patterns of climate connectivity, which we define as whether the spatial configuration of natural lands allows species to track their current climatic conditions during projected climate change. Using this metric, we can address the fundamental question of where and by how much habitat fragmentation is limiting species’ ability to traverse climate gradients in the face of climate change. Our research incorporates land use patterns to ask how far species could potentially move across the current configuration of natural lands and if it is far enough to track projected temperature changes. We are not asking if species will have the innate capacity to survive climate change. Rather, we ask whether, where, and by how much the structural connectivity of natural lands will allow species dispersal to suitable climates.

Once we know the limitations imposed by habitat fragmentation, we go on to assess the most effective way to facilitate climate connectivity. Increasing connectivity among natural areas is the most commonly recommended strategy to mitigate climate change effects on biodiversity (10). Introducing habitat corridors or otherwise increasing landscape permeability promotes the admixture of populations and allows those populations to redistribute as their environment changes (11). Several studies indicate that habitat corridors promote faunal movement (12 and refs. 13 and 14 and references therein). However, no one has systematically evaluated the efficacy of this strategy for promoting dispersal in response to climate change. Here, we ask how and where corridor establishment could lead to an increased ability to track climate.

Approach

Our first step in evaluating climate connectivity was to identify the most natural tracts of land remaining within the contiguous United States (a flow chart describing our approach is provided in Fig. S1). Our analysis identifies 45% of the geographic area of the contiguous United States as natural (Fig. 1 and Fig. S2). To identify these natural regions, we used published human modification data (15, 16), which quantifies how much humans have altered the landscape by integrating data about land use, land cover, and road proximity. We identified natural regions as land having human modification values (H) less than or equal to 0.37, the 90th percentile of values from currently protected lands [status levels 1 and 2 in the Protected Area Database (17)]. We


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Significance

Many plants and animals will need to move large distances to track preferred climates, but fragmentation and barriers limit their movements. We asked to what degree and where species will be able to track suitable climates. We demonstrate that only 41% of US natural land area is currently connected enough to allow species to track preferred temperatures as the planet warms over the next 100 years. If corridors allowed movement between all natural areas, species living in 65% of natural area could track their current climates, allowing them to adjust to 2.7 °C more temperature change. The greatest benefits result from connecting low-lying natural areas, especially in the southeastern United States. Facilitating movement will be crucial for preventing biodiversity losses.

Supporting Online Material

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partitioned these natural regions into patches characterized by 1 °C increments (Fig. S2). Using these temperature-partitioned patches, we identified the coolest destination patch to which any origin patch is connected, following a series of hotter to cooler patches via adjacent natural patches (Fig. S3). We calculated how much cooler the destination patch was than the origin patch (Fig. S4), and whether this difference exceeded temperature changes projected for the origin patch [using the average of temperature projections from 15 general circulation models run for the A2 emissions scenario (18) for the years 2050–2099 (19); Fig. 1, Figs. S1 and S2, and Tables S1 and S2; other emission scenario results are reported in Tables S1 and S2]. In these analyses, we used mean annual temperature (MAT; hereafter temperature) as the target climate variable.

Results and Discussion

Only 41% of natural land area achieves climate connectivity if movement is assumed only to occur between a series of adjacent natural patches (Fig. 1A and Table S1). The western United States has higher climate connectivity (51% of natural land area) compared with the eastern United States (2% of natural land area) (Fig. 2 and Table S1; the east-west division is illustrated in Fig. S5). Once we established this baseline, we asked to what degree increasing connectivity by adding corridors between natural patches increases climate connectivity and where establishing corridors would be most effective.

Climate-gradient corridors identify movement routes between patches that follow monotonically decreasing temperature gradients while simultaneously minimizing cumulative resistance to movement (20). Resistance increases with degree of human impact (movement cost) and climate gradient steepness or reversal (Methods and Eq. 1). Urban centers impose high traversal costs, whereas minimally disturbed areas are more conducive to traversal. Using this method, we created climate-gradient corridors for the contiguous United States (Fig. 3, SI Methods, and Figs. S1 and S6).

Introducing corridors between patches separated by up to 100 km of human-impacted ($H > 0.37$) land increases nationwide climate connectivity to 65% of natural land area and allows species living in natural patches to adjust to a median of 2.7 °C more temperature change (Fig. 1B and Tables S1 and S2). If we limit maximum corridor length to 10 km, we still achieve climate connectivity for 60% of natural land area. Adding corridors increases climate connectivity in the western and eastern United States by similar percentage points of natural land area (24%...
and 25%, respectively), resulting in more success in the West (75%) than the East (27%) (Fig. 2, Figs. S5 and S7, and Table S1).

We would not have expected proportional improvement in climate connectivity to be similar in the eastern and western United States (Figs. 1 and 2), given that temperatures are projected to increase more in the West (Fig. S2B). However, the West also contains colder mountain ranges and steeper climate gradients (Fig. S24). Cold regions provide target destinations for tracking changing climate, allowing species living in temperate areas that are projected to warm to achieve climate parity even after the entire landscape warms. The lack of natural lands and the basin of higher temperatures in the Midwest (Fig. S24) prevent movement between the East and West or into the north-central regions, where cool, natural land patches persist.

When assessing climate connectivity by ecoregion, we find that connecting low-elevation regions, notably the semiarid prairies and coastal plains, provides the greatest improvement from corridors (Figs. 1 and 2; ecoregion names and locations are provided in Fig. S5). The west and south-central semiarid prairies experience large increases in climate connectivity (56 and 47 percentage point increased climate connectivity area) when fragmented natural regions are connected to the cool Western Cordillera region (Figs. 1 and 2). The Texas-Louisiana coastal plains and Mississippi alluvial and southeast coastal plains experience improvements (64 and 57 percentage point increased climate connectivity area) through connections into the Ozark, Ouachita, and Appalachian mountain systems (Figs. 1 and 2). The smallest improvements from corridors are seen in two types of areas: (i) ecoregions distant from cool montane regions, such as the Everglades, the central plains, or the temperate prairies (0, 2, and 10 percentage point increased climate connectivity area) or (ii) certain montane regions, including the Western Cordillera and Western Sierra Madre (4 and 10 percentage point increased climate connectivity area), where natural regions are already adjacent and mountaintops create climate islands (Figs. 1 and 2 and Fig. S7).

To evaluate the differences in benefits among corridor placements further, we explored where corridors would be least challenging to construct. We examined cumulative resistance and corridor efficiency. We define cumulative resistance as the summed total of all cost-weighted distances of the corridors necessary to reach the cool destination patch and corridor efficiency as the cumulative resistance per kilometer of corridor. Corridor efficiency thus represents a combination of human impact and temperature gradients. More efficient corridors are less challenging to traverse and may be less expensive to purchase, conserve, and restore, because they generally have lower human impacts. Here, we assess only those patches that could achieve climate connectivity because of corridors.

Average cumulative resistance of eastern climate corridors is 4.3-fold higher than western corridors (Welch’s $t = 28.8$, df = 1455, $P < 0.0001$). However, corridor efficiency in the East is 0.89-fold corridor efficiency in the West (Welch’s $t = -18.4$, df = 2622, $P < 0.0001$; Fig. 3). Thus, eastern corridors cross less intensely human-impacted land and/or shallower climate gradients but across longer corridor distances (Fig. 3). This finding is further demonstrated by restricting corridor length to 10 km, where eastern climate connectivity success drops from 27 to 16%.

Similarly, ecoregions with the highest cumulative resistance are also most benefited by corridors. Three southeastern ecoregions, the Mississippi alluvial and southeast coastal plains, Texas-Louisiana coastal plain, and west and south central semiarid prairies, contribute 65% of total cumulative resistance across all 20 ecoregions (Fig. 2 and Fig. S5) but also have the best corridor efficiency (Fig. 3).

Eastern corridors, particularly in those three southeastern ecoregions, have a larger proportional impact and demonstrate better corridor efficiency (Fig. 3). Climate connectivity increases by 13-fold in the East (from 2 to 27%), and this increase may be

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**Fig. 2.** Percentage of natural area per ecoregion that succeeds at achieving climate connectivity. Orange colors are western ecoregions; teal colors are eastern ecoregions. Bright colors are climate connectivity success, given adjacency only; pale colors are the additional success given corridors; and dark colors are failures. Bar width indicates the natural area per ecoregion, and bars are sorted by decreasing success, given adjacency only. Three missing ecoregions contained too little natural area to display: Everglades (0% adjacent success, 0% corridor success), central plains (0% adjacent success, 1.6% corridor success), and temperate prairies (0.1% adjacent success, 10% corridor success). (Inset) Overall success rates in the West vs. East. Ecoregion locations and the east-west division are provided in Fig. S5.
more critical for overall dispersal than the 0.5-fold increase in the West (51–75%) (Figs. 1 and 2, Fig. S7, and Table S1). Moreover, based on projected species range shifts, many more individual vertebrate species will likely need to track suitable climates through the southeastern United States and Appalachian Mountains than through the western mountain systems (21). In particular, the regions that have both the highest improvement with corridors and a high volume of vertebrates needing to traverse that landscape (21) are the coastal plains of Texas, Louisiana, Mississippi, and the southeastern United States (Figs. 1–3 and Fig. S5).

Under projected climate scenarios, corridors will be a critical strategy for allowing species to respond to warmer temperatures (Fig. S7). The A2 emissions scenario used here is moderate, comparable to representative concentration pathway 4.5 (RCP4.5) (Tables S1 and S2). If climate change is more severe, even corridor-assisted connectivity may be insufficient, because hotter temperatures produce fewer, smaller cool destinations for species (Tables S1 and S2). Additionally, the natural land patches we identified provide large tracts of land and many small, intermediate patches to serve as steppingstones (Fig. S24). However, as human impacts increase, these steppingstones may disappear (22–24).

Climate connectivity does not guarantee species persistence in the face of climate change. High connectivity only provides the potential for species to disperse to temperatures similar to those temperatures they experience today. Destination patches may be too small to allow sufficient population sizes for survival (25–27). Also, temperatures are changing so rapidly that even species with the potential to disperse may still not disperse quickly enough to reach future areas of climate suitability (28–30).

However, even without increasing connectivity, our findings do not necessarily portend wide-scale extinctions. Many species have relatively broad temperature tolerances and may survive even hotter conditions than they occupy today. Species may also evolve or undergo phenotypically plastic shifts to enable further survival. Our analyses likely underestimate the ability of many climate-limited species to persist in cooler microhabitats (31–33), which our 1-km² spatial resolution with 10-km² minimum patch sizes may be too coarse to identify. This issue of spatial resolution is especially relevant in montane regions, where climate variation is high, and small regions with different temperatures were necessarily lumped to create 10-km² patches. The use of MAT as our climate variable of interest may also obscure important climate-driven impacts for certain habitats or certain types of species. For example, in California, the strong seasonal fluctuations characteristic of this region’s Mediterranean climate mean that the use of the MAT climate variable could obscure the more relevant changes in seasonal climatic variation in this region (34). Analyses that focus on species movement needs with respect to small-scale variation and diverse climate variables could lead to more optimistic results.

Under rapidly changing climatic conditions, in which many species must adapt or move to preclude extinction, fragmentation limits one critical coping strategy. Of course, human-impacted land does not hinder all organisms. Some birds or wind-dispersed seeds and insects may be able to traverse hundreds of kilometers of inhospitable lands, but even these species’ movements are made easier by the introduction of corridors (35–37). Those species that struggle with dispersal across roads, through cities, and across agricultural fields (e.g., many amphibians, reptiles, plants, small mammals) need an alternate solution. Knowing where to focus conservation efforts is crucial for these species and for the future of biodiversity. We find that corridors will be critical for movement, given high habitat fragmentation levels. This need is particularly critical in the southeastern United States and regions with fragmented landscapes and few nearby climatic refuges. Facilitating movement between natural lands will greatly improve the chances of species being able to track suitable climates.

**Methods**

Our study area includes the contiguous United States buffered by 100 km into Mexico and Canada. We performed all statistical analyses on the contiguous United States only. We analyzed maps at 1-km resolution, projected into North American Datum (NAD) 1983 Albers equal area conic projections. An outline of all methods can be seen in Fig. S1.

**Identifying and Climate-Partitioning Natural Patches.** To identify natural regions, we used a map that depicts human impacts by quantifying the degree of human modification (H) with values ranging from 0–1.0 (low to high) (15). This map combines nearly a dozen layers of anthropogenic stressors with empirical validation to create a layer for the contiguous United States that integrates data about land use, land cover, and road proximity (15). It has been thoroughly vetted to establish consistent values nationwide, but does not extend beyond the borders of the contiguous United States [details are provided by Theobald (15)]. Not wanting to truncate climate gradients artificially at political borders, we used a 100-km buffer extending into Canada and Mexico using the Human Influence Index (HII) map (16). The HII map does not integrate the full set of...
Future Temperature Projections. To evaluate climate connectivity, we report results for the mean ensemble of 15 models for a future (2050–2099) time period [A2 emission scenario (18); continually increasing rate of greenhouse gas emissions] (19). We use mean current MAT (1950–2000) and mean future MAT (2050–2099) for all primary calculations. Those layers were then subtracted to create a map of projected temperature change (Fig. S2B) that was used in conjunction with the current WorldClim dataset. A version of the WorldClim dataset was completed for Interdisciplinary Research on Climate 5 (MIROC5) models of four RCP scenarios: RCP2.6, RCP4.5, RCP6.0, and RCP8.5 (40).
the destination temperature, given the patch connectivity ($T_{pk}$; Fig. S3). In addition, we calculated cumulative resistance for each patch by summing the costs of the corridors used to achieve each patch’s destination. No cost was assigned for using adjacent patches.

To determine which patches achieve climate connectivity given patch adjacency and corridor connectivity, we used these newly calculated destination temperatures ($T_{pk}$) to calculate the margin of success or failure at climate connectivity ($\Delta T_{pk}$, Fig. 18 and Fig. S1). If the margin of success or failure is positive, climate connectivity is achieved, meaning that organisms living in that patch could track their current temperatures through a combination of adjacent patches and corridors, given projected climate change.

We again calculated success rates and median and first and third quartile temperature margins ($\Delta T_{pk}$) that would occur under five emission scenarios (Tables S1 and S2). Additionally, we calculated success rates for a scenario in which corridors are ≤10 km in length for the A2 emission scenario. Including only these shorter corridors decreased the percentage points of natural land area that succeeds at achieving climate connectivity by 4% in the West, 11% in the East, and 5% overall.

Geographic Analyses of Climate Connectivity. Our final map identifies the patches that failed to achieve climate connectivity, given adjacency alone, but then succeeded once corridors were introduced (Fig. S7).

We compared the number of patches, the potential for temperature change achievable, and the margins of success or failure in the eastern vs. western United States (Fig. 2 and Tables S1 and S2). We performed t-tests to estimate where differences were significant. For these analyses, the contiguous United States was divided at 100°W longitude, which has long been held as a general dividing line between the more arid, western United States and the moister East and the resultant disparities in human settlement patterns (45, 46) (Fig. S5). We additionally compared the temperature changes achievable and the margins of success or failure within level II Environmental Protection Agency ecological regions (47) (Fig. 2 and Fig. S5).

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