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Maximum temperatures determine the habitat affiliations of North American mammals

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Addressing the ongoing biodiversity crisis requires identifying the winners and losers of global change. Species are often categorized based on how they respond to habitat loss; for example, species restricted to natural environments, those that most often occur in anthropogenic habitats, and generalists that do well in both. However, species might switch habitat affiliations across time and space: an organism may venture into human-modified areas in benign regions but retreat into thermally buffered forested habitats in areas with high temperatures. Here, we apply community occupancy models to a large-scale camera trapping dataset with 29 mammal species distributed over 2,485 sites across the continental United States, to ask three questions. First, are species' responses to forest and anthropogenic habitats consistent across continental scales? Second, do macroclimatic conditions explain spatial variation in species responses to land use? Third, can species traits elucidate which taxa are most likely to show climate-dependent habitat associations? We found that all species exhibited significant spatial variation in how they respond to land-use, tending to avoid anthropogenic areas and increasingly use forests in hotter regions. In the hottest regions, species occupancy was 50% higher in forested compared to open habitats, whereas in the coldest regions, the trend reversed. Larger species with larger ranges, herbivores, and primary predators were more likely to change their habitat affiliations than top predators, which consistently affiliated with high forest cover. Our findings suggest that climatic conditions influence species' space-use and that maintaining forest cover can help protect mammals from warming climates.

mammal community | climate change | occupancy | biodiversity conservation | habitat loss

Habitat conversion is reducing terrestrial biodiversity and transforming ecological communities worldwide (1, 2). Though many species are able to persist in the farms, towns, and production forests that typify modern working landscapes (3), the communities that occupy natural versus anthropogenic landscapes are often distinct (2). Much effort has been expended to quantify interspecific variation in species responses to habitat change and, in doing so, identify the "winners" and "losers" associated with ongoing global change (4–7). For example, classic studies placed North American birds and mammals into three categories based on the degree to which they are preadapted to persist in urban areas: urban adapters (i.e., species that now heavily utilize anthropogenic habitats), urban avoiders (i.e., those that are restricted to natural environments), and urban exploiters (i.e., habitat generalists that can exploit both anthropogenic and natural areas) (8, 9).

However, recent evidence suggests that species are not monolithic with respect to their tolerance of anthropogenic habitats. That is, populations of the same species may exhibit very distinct responses to anthropogenic land-use in different regions (10). For example, birds in the Atlantic Forests of Brazil appear to be more sensitive to deforestation near the edge of their ranges compared to their range centers (11). Thus, placing species into simple categories, such as avoiders, adapters, and exploiters, may mask substantial variation in how species respond to habitat conversion.

Though the intraspecific variation in species responses to habitat conversion is rarely quantified, many nonmutually exclusive mechanisms may cause different populations of the same species to use anthropogenic habitats in some regions but not others. First, populations may have adapted to anthropogenic landscapes in regions with a long history of anthropogenic modification but not in more recently impacted areas (12–14). Second, some populations may persist in anthropogenic landscapes by regularly receiving colonists from nearby natural areas, i.e., via source-sink dynamics (15, 16). Third, anthropogenic landscapes vary across space, in terms of both intensity of development and the patterns of fragmentation, with some landscapes composed of heterogeneous mosaics of diversified farms and small settlements, where many organisms can thrive,

Significance

While many studies have explored the effects of climate and land-use change in isolation, few have investigated how they interactively affect mammal distributions. If climatic conditions dictate species' capacities to persist in anthropogenic landscapes, increasing temperature and precipitation variability may impede efforts to conserve biodiversity in anthropogenic landscapes. We leveraged a continental-scale dataset to study variation in how North American mammals respond to forest cover and anthropogenic modification across their ranges. Species were consistently more sensitive to human modification, and more dependent on forests, in hotter regions. This suggests that decisions about enhancing the conservation value of anthropogenic landscapes versus protecting natural areas should consider how species' habitat affiliations are likely to shift under a changing climate.

versus others dominated by large cities and intensive agriculture, where biodiversity often plummets (3, 17).

Yet another possibility is that species' climatic niches constrain their ability to use anthropogenic landscapes in some regions but not others (18, 19). When temperatures spike (or plummet), many species can behaviorally thermoregulate by seeking thermally buffered microclimates (20). The presence of suitable microclimates can therefore drive species' distributions (21), allowing species to persist in areas that would otherwise regularly exceed their thermal tolerances. Critically, anthropogenic land-uses are often much more structurally homogeneous than natural areas, resulting in reduced thermal buffering capacity and fewer potential climate refugia (20, 22–24). For example, converting shaded tropical forests to open agricultural fields can cause local temperatures to increase by over 10 °C relative to nearby shaded forests (25, 26). Habitat conversion can also alter moisture regimes, either causing declines in moisture availability, for example, by removing tree canopies and drying the understory, or increases in moisture availability through irrigation (27). Correspondingly, several studies suggest that species may switch their habitat affiliations along macroclimatic gradients. For example, Neotropical herpetofauna are more likely to occupy agriculture at higher elevations because low-elevation sites regularly experience much more severe local temperature spikes (28, 29). Similarly, tropical birds seem to shift their habitat affiliations along climate gradients, using anthropogenic habitats more often in wetter (30, 31) or more seasonal regions (32).

If climatic conditions dictate species' capacities to persist in anthropogenic landscapes, then increasingly frequent and severe temperature spikes and precipitation variability (33) may impede efforts to conserve biodiversity in anthropogenic landscapes (3). At the same time, identifying contexts in which species may be able to use working landscapes—both now and with ongoing climate change—may help improve the efficacy of farmland biodiversity conservation programs (34). However, while many studies have explored the effects of climate and land-use in isolation, the interactive effects of climate and land-use change are less understood yet likely a primary driver of species distributions in the Anthropocene (26, 35, 36).

We leveraged a continental-scale mammal monitoring program to study intraspecific variation in terrestrial mammal responses to forest cover and human modification. Our work was guided by three questions. First, are species' use of forest and anthropogenic habitats consistent across continental scales? We predicted that, although some species always avoid or affiliate with anthropogenic habitats, some will affiliate with anthropogenic habitats in some regions and natural habitats in others. Second, do macroclimatic conditions explain spatial variation in species responses to land-use? We predicted that mammals use forests more often—and anthropogenic habitats less often—in drier regions and in regions with hotter temperature because forests can thermally buffer the understory and retain moisture in dry areas (27). Finally, can species traits elucidate which species are most likely to show climate-dependent habitat associations? We predicted that climate-dependent habitat associations would be more common in a) herbivores and primary predators because top predators may be especially persecuted by humans and thus sensitive to human modification everywhere (37), b) diurnal species because high temperatures in anthropogenic habitats are tempered at night, c) large-bodied species, because physiological cooling costs often increase with body size (38), and d) narrow-ranging species because, on the one hand, they are often assumed to have narrow abiotic tolerances (39) and

thus may need to switch their habitat affiliations to cope with thermal extremes. On the other hand, however, narrow-ranged species are also often ecological specialists and thus may be unable to shift their habitat preferences across different regions.

Results

We analyzed camera trap data collected in 2019 and 2020, consisting of over 150,000 presence records of 29 species across 2,485 sites (camera trap locations) and covering a gradient of land-cover types and climatic conditions (*SI Appendix*, Tables S1–S4). First, we generated a hexagonal grid across the continental United States (453 cells of >10,000 km^2), and selected grid cells with at least one camera trap deployment (122 grid cells with 1 to 153 camera locations per cell; *SI Appendix*, Fig. S1). We then built community occupancy models that account for imperfect detection to 1) quantify intraspecific variation in mammalian response to land-cover among grid cells, 2) determine whether macroclimatic conditions explain spatial variation in responses to land-cover, and 3) assess whether species traits elucidate which species exhibit interactions between climate and land-cover.

Variability in Response to Land-Cover. In model set 1, we assessed intraspecific variation in species' responses to land-cover by modeling responses as a random effect over grid cells and using the random effect SD as a measure of that variation. We found that species' responses to both land-cover variables (i.e., forest proportion and human modification) varied strongly and significantly across their US ranges. At the community level, the probability of occupancy did not systematically increase or decline in response to forest proportions (μ_{forest} = −0.12; 90% Bayesian credible intervals, BCI: −0.4 to 0.1) or human modification ($\mu_{modification}$ = 0.13; 90% BCI: −0.35 to 0.6). Average species-level effects (i.e., average effects across all hexagons within a species' US range) indicated that four species responded significantly positively and ten species responded significantly negatively to forest proportions. Likewise, nine species responded positively and three species responded negatively to human modifications. Based on the proportion of hexagons with negative/positive coefficients for land-cover, we classified five species as forest specialists (positive response in at least 75% of grid cells), five species as open specialists (negative response in at least 75% of grid cells), and 19 species as generalists. With respect to human modifications, six species were human affiliated (positive response in at least 75% of grid cells), five species were nature affiliated (negative response in at least 75% of grid cells), and 18 species were generalists.

These average responses, however, masked significant variations in how species responded to land-use across their ranges. At the community level, the variation across hexagonal grid cells in the community response to forest (σ_{forest}) was 1.8 (90% BCI: 0.6 to 5.7) and to human modification ($\sigma_{modification}$) was 2 (90% BCI: 0.1 to 8.8). Similarly, SDs across hexagonal grid cells for species-specific responses to forest cover and human modification (ω_{Lk}) were above 1 for all species, and the 90% highest posterior density (HPD) for all species did not include zero (Fig. 1). Species that exhibited more spatial variation in their responses to forest cover also tended to exhibit more variation in their response to human modification (Fig. 1; Spearman's rank correlation coefficient = 0.82). Together, these results indicate that North American mammals exhibit
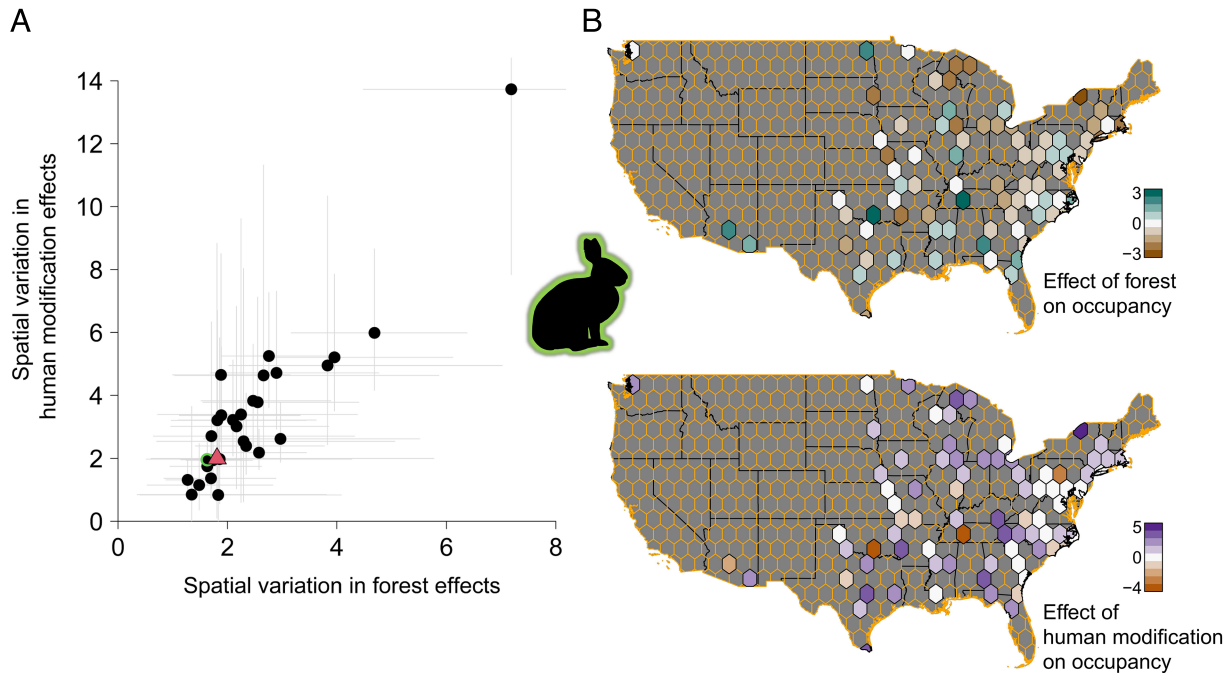
Fig. 1. Spatial variation in land-cover effects on mammal space-use. (*A*) SD of land-cover effects on species probability of site use, estimated by a community occupancy model fit to camera-trap data of 29 species (black circles). Circles show the posterior mode of species-specific parameters—i.e., how a species' response to land-cover varies across the species distribution within the United States; the red triangle indicates the mode community average coefficient. Gray lines show 90% Bayesian credible intervals. (*B*) Maps depict spatial variation in land-cover responses for the eastern cottontail *Sylvilagus floridanus*, as an example. Each grid cell is colored according to the predicted effect of land-cover on occupancy probability, as calculated by adding the estimates of the species-specific average response to the species-specific spatial random effect of hexagons in our occupancy model. The *Top* map shows cells in which forest cover is estimated to increase (green), have no effect on (white), or decrease (brown) cottontail occupancy. The *Bottom* map shows areas of positive (purple), neutral (white), and negative (brown) effects of human modification on occupancy. The eastern cottontail is also highlighted with a green outline in panel *A*.

significant intraspecific variation in land-cover responses across space.

Climate-Dependent Response to Land-Cover. In model set 2, we used interactions between climate and land-use variables to assess whether climate mediates variation in species' response to land-cover. We found that macroclimatic conditions mediated species' responses to forest cover and human modification across their US ranges, with the maximum temperature of the warmest month being the strongest climatic predictor of species' land-cover associations. In locations with higher maximum temperatures, on average, species space-use was more associated with forested habitats and more sensitive to human modification (Figs. 2 and 3, and *SI Appendix*, Figs. S2–S4). Specifically, in hot regions (i.e., maximum temperature of 40 °C), models predicted that increasing forest proportion from 0 to 1 or decreasing human-modified area from 0.8 to 0 would result in a 50% and 66.7% increase in occupancy for the average mammal. However, in cooler regions (i.e., maximum temperature of 20 °C), increasing forest cover and decreasing human-modified areas by the same amount would decrease average mammal occupancy by 55% and 42.1%.

Occupancy models from model set 2 also provided insight into which species were most likely to change their associations with forest or human-modified lands across macroclimatic gradients (*SI Appendix*, Figs. S3 and S4 and Table S5). Eleven of the 29 species in the community were significantly more forest affiliated in hotter regions (i.e., the 90% BCI of the interaction term did not include 0). This included both forest specialist species (as defined by results from model set 1) that became even more affiliated with forests in hot regions (e.g., puma *Puma concolor*) and generalist species, which were forest affiliated in hot

regions and open-habitat affiliated in cooler regions (e.g., eastern gray squirrel *Sciurus carolinensis*). No species were significantly more forest affiliated in cooler regions, and 18 species did not significantly change their association with forest cover across the temperature gradient. Correspondingly, in hotter regions, eight species were significantly less associated with human-modified areas and 20 species did not change their association with human modification. Only one species (mule deer *Odocoileus hemionus*) showed the reverse trend, exhibiting a positive association with human modification in hotter regions and negative associations in cooler regions.

Trends in relationships with average annual temperatures mimicked those in maximum temperatures at the species level but were not significant at the community level (*SI Appendix*, Table S6). In contrast, land-use did not interact with minimum temperatures to affect species or community-level space-use. For precipitation, there were no community-level responses; that is, on average across the community, species were no more likely to use forests or human-modified areas in wetter versus drier regions. That said, some species did exhibit significant interactions between land-cover and precipitation (*SI Appendix*, Table S5). Specifically, eight of the 29 species in the community were significantly more forest affiliated in dry regions (i.e., had a significant negative interaction term). This included both forest specialist species (as defined by results from model set 1) that became even more affiliated with forests in dry regions (two species, puma and mule deer), and generalist species, which were forest affiliated in dry regions and open-habitat affiliated in wetter regions (six species, e.g., Virginia opossum *Didelphis virginiana*). On the other hand, four species were significantly more forest affiliated in wetter regions (i.e., had a significant positive interaction term; e.g., fox squirrel *Sciurus niger*), and

17 species did not significantly change their association with forest cover across the precipitation gradient. Correspondingly, in dry regions, five species were significantly less associated with human-modified areas (e.g., elk *Cervus canadensis*), 20 species did not significantly change their habitat associations, and four species (e.g., mule deer) showed the reverse trend, exhibiting positive association with human modification in drier regions and negative associations in wetter regions.

Effects of Traits on Interactions between Land Cover and Climate. In model set 3, we assessed whether species' traits explain the interaction strength between climate and land-cover using three-way interactions. We found mixed evidence that species traits could elucidate which species were most likely to exhibit interactive effects of land-use and maximum temperature on occupancy (*SI Appendix,* Table S7). Specifically, diurnal species were more likely to shift their affiliations with anthropogenic habitats across maximum temperature gradients, compared to species with nocturnal or crepuscular activity patterns ($\beta_{TCmodification} = -0.49$; 90% BCI: -0.91 to -0.07). However, neither trophic level, body mass, nor range size
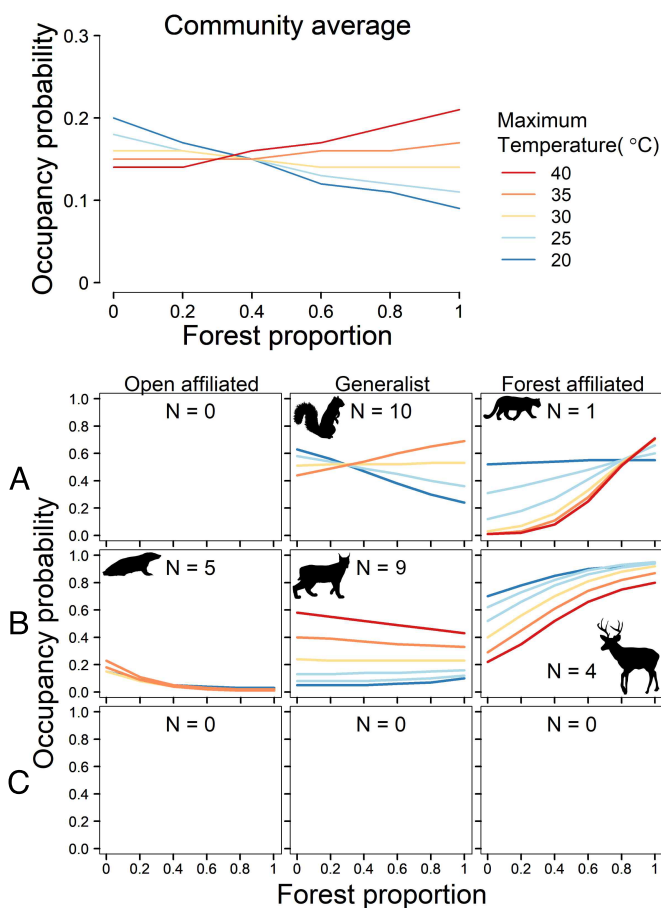

Fig. 2. Interactions between land-use and climate for terrestrial mammal communities (29 species) across the contiguous United States, predicted by a community occupancy model. In hotter regions, the community became more forest-affiliated (*Top* plot). Eleven species (eastern gray squirrel *Sciurus carolinensis* and puma *Puma concolor* are shown as examples) were more forest affiliated in hotter regions (*A*), whereas 18 species (e.g., American badger *Taxidea taxus*, bobcat *Lynx rufus*, and white-tailed deer *Odocoileus virginianus*) were consistent in their forest affiliations across the maximum temperature gradient (*B*). There were no species that became less forest affiliated in hotter regions (*C*). Colors represent maximum temperatures of the warmest months.
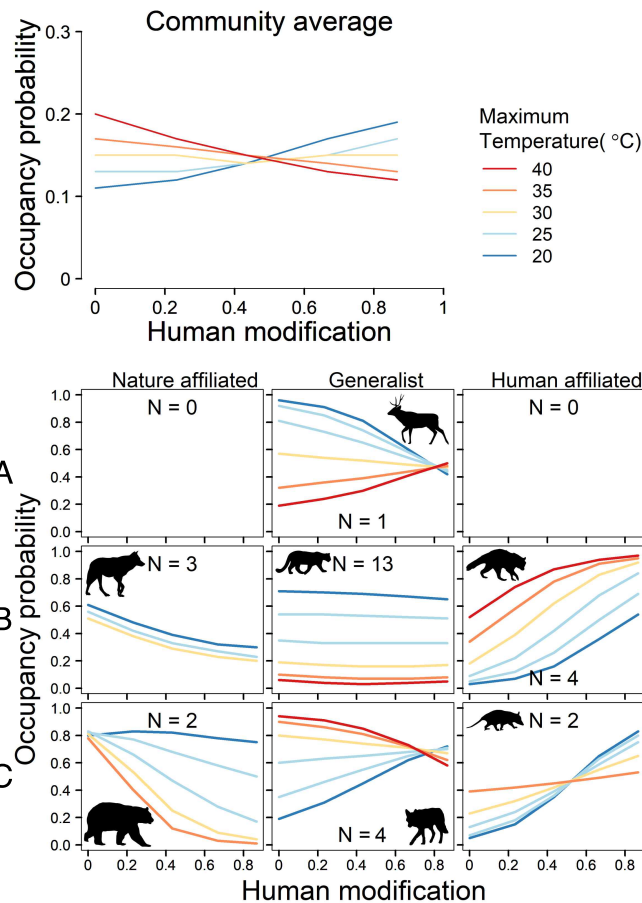

Fig. 3. Maximum temperatures mediate mammal species responses to human modification. In hotter regions, the community became less affiliated with anthropogenic habitats (*Top*). One species (mule deer *Odocoileus hemionus*) became more affiliated with anthropogenic habitat in hotter regions (*A*), 20 species (e.g., gray wolf *Canis lupus*, puma *Puma concolor*, and raccoon *Procyon lotor*) were consistent in their habitat affiliations across the maximum temperature gradient (*B*), and eight species (e.g., black bear *Ursus americanus*, coyote *Canis latrans*, and Virginia opossum *Didelphis virginiana*) became less affiliated with anthropogenic habitats in hotter regions (*C*). Colors represent maximum temperatures of the warmest months.

affected interactions between maximum temperature and human modification (*SI Appendix,* Table S7). In contrast, species with larger body masses were more likely to shift their affiliations with forest cover across maximum temperature gradients ($\beta_{TCforest} = 0.20$; 90% BCI: 0.0 to 0.43). There was also a tendency for species with larger range sizes and herbivores and primary predators to be more likely to shift their affiliations with forest cover across maximum temperature gradients ($\beta_{TCforest} = 0.18$; 90% BCI: -0.04 to 0.42 and $\beta_{TCforest} = -0.37$; 90% BCI: -0.76 to 0.01 for range size and trophic levels, respectively) compared to top predators, which were more consistently affiliated with high forest cover across their ranges (Fig. 4). Finally, unlike for human modification, temporal activity patterns did not influence interactions between maximum temperature and forest cover.

Discussion

Our results suggest that intraspecific variation in habitat preferences is pervasive among North American mammals, with all studied species exhibiting significant spatial variability in their use of forests and human-modified habitats across the continent. Specifically, we found that mammals switch their
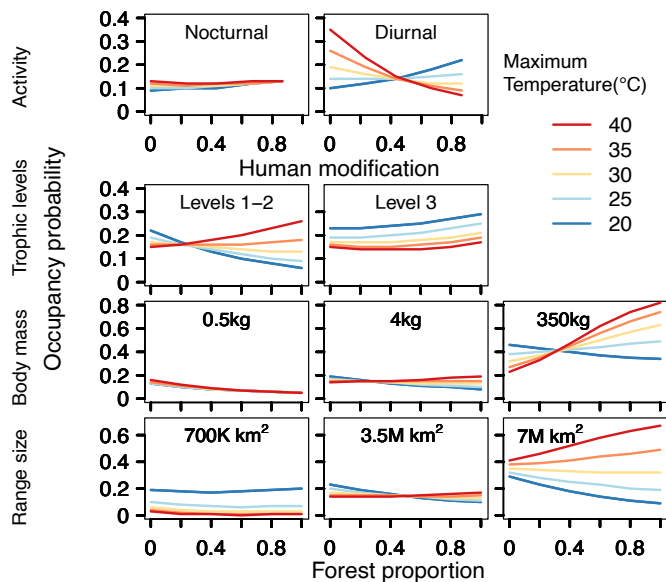
Fig. 4. Interactions between land-cover and maximum temperatures may be partially mediated by species traits. The plots show how the probability of occupancy changes with forest proportions and human modifications in areas with different maximum temperatures. Responses are predicted by four community occupancy models with a three-way interaction term between forest cover or human modification, maximum temperatures, and each trait. Thus, the plots show marginal, and not conditional, effects. Species range size and body mass are continuous (and predictions are graphed at 3 discrete levels). Trophic level (herbivores and primary predators—i.e., levels 1 and 2, versus top predators—i.e., level 3) and activity time are binary (diurnal and cathemeral versus nocturnal and crepuscular). Models suggest herbivores, primary predators, species with larger range sizes, and larger species may be more likely to exhibit forest-climate interactions. Likewise, species with diurnal activity patterns are more likely to exhibit interactions between human modification and temperatures.

habitat affiliations to become more associated with forests and more sensitive to human modification in warmer regions. Species traits partly elucidated which species were most likely to exhibit significant interactions between land-use and climate, with larger, wider-ranging, and diurnal herbivores and primary predators more likely to use forests or avoid human-modified habitats in warmer regions.

Intraspecific Variation in Mammalian Responses to Land–Cover. Though much research has sought to guide conservation priorities by characterizing which species are likely to thrive versus decline in human-modified habitats (5–7), intraspecific variation in species responses is only beginning to be acknowledged in macroecological studies (10). Our results suggest grouping species into broad categories—such as urban avoiders, adapters, and exploiters—may mask substantial variation in how species respond to habitat conversion. In some senses, this finding is unsurprising: Population-level space-use is the outcome of individual habitat-use decisions, and the resource/habitat selection literature is replete with examples of individuals exhibiting different habitat selection strategies (40) due to intrinsic, e.g., sex; (41) and extrinsic, e.g., habitat availability; (42) factors.

Nonetheless, failing to recognize that populations exhibit predictable variability in habitat preferences across space has important implications for conservation (43). On the one hand, environmental managers may divert resources toward improving human-modified landscapes in areas where species are largely restricted to natural habitats. On the other hand, assuming a species will always be restricted to natural areas may lead

to missed opportunities for conserving biodiversity alongside people: for example, by planting hedgerows, retaining small patches of natural habitats, or reducing agrochemical applications in human-modified landscapes (3).

Maximum Temperatures Mediate Mammalian Responses to Land-Cover. Maximum temperatures, much more so than average temperatures or minimum temperatures, played a key role in determining how species respond to forest cover and human modification. As noted, closed forest canopies can thermally buffer the understory, thereby guarding against regional climate extremes (44). In contrast, many anthropogenic habitats lack closed canopies and thus also lack the local thermal buffering capacity needed to provide organisms with climate refugia (20, 22–24). The microclimate buffering hypothesis posits that species' habitat preferences may be at least partially driven by variations in climate buffering capacities among habitat types (22). Correspondingly, multiple tracking studies have shown that large mammals change their habitat selection preferences during heat waves. For example, moose *Alces alces* increasingly occupied forests, and ibex *Capra ibex* moved upslope when temperatures spiked (45, 46). Birds too are known to occupy more shaded areas within their home ranges during heat waves (47, 48). Behavioral thermoregulation is also a well-known phenomenon among herpetofauna, though temperature-induced changes in habitat use often occur at smaller scales, e.g., retreating into shade, burrows, or tree crevices (49, 50). In particularly warm regions, organisms may thus pre-emptively increase their use of thermally buffered habitats—as we report here—because in open areas without microclimate refugia, heat waves would exact direct physiological stress on organisms (e.g., hyperthermia), and limit their activity times, thus preventing organisms from foraging or reproducing (38, 51, 52). Another possibility is that temperature spikes may aggravate already lower resource availability in human-modified areas, causing organisms to retreat into natural habitats (53–55).

Unlike maximum temperatures, we found precipitation gradients to have mixed effects on species' habitat preferences. We had hypothesized that higher moisture availability in forests might cause species to specialize in forests in drier regions (27), as seems to be the case for some Neotropical birds (30). However, we observed no significant interactions between habitat affiliation and precipitation at the community level. At the species level, we found eight species were more forest affiliated and five species were less human-affiliated in dry regions, aligning with our initial hypothesis. However, four and four species exhibited the reverse trend, becoming less forest affiliated and more human-affiliated in dry regions. Some of this variation could be due to anthropogenic water subsidies: In dry regions, irrigated agriculture or residential yards may actually have more moisture availability than nearby natural areas. Indeed, several studies have shown that anthropogenic water subsidies during drought or in dry regions can strongly influence wildlife distributions (56, 57).

Traits Explain Some Variation in Interactions between Climate and Land-Use. Our results suggest that some species exhibit more intraspecific variation in habitat preferences than others and species that tend to be more spatially variable in their forest affiliation are also more spatially variable in their sensitivity to anthropogenic modification. The traits we examined exhibited some explanatory power in differentiating species that were more versus less likely to exhibit significant interactions between climate and land-use and generally confirmed our expectations.

First, larger species showed stronger interactions between maximum temperatures and forest cover. This may be because larger species tend to have increased cooling costs and thus face greater difficulties thermoregulating (38). Second, top predators showed marginally weaker interactions between maximum temperatures and forest cover than herbivores or primary predators, likely because top predators are often more subject to human persecution and thus relatively sensitive to human modification and more restricted to forest habitat everywhere (37). Third, species with larger ranges showed marginally stronger interactions between maximum temperatures and forest cover, lending support for the possibility that small-ranged species may be so specialized that they are unable to shift their habitat preferences in different regions (39). We had originally hypothesized that narrow-ranged species might be more likely to shift their habitat affiliations across thermal gradients as small ranges can be associated with narrow thermal tolerances. Future work might look at thermal tolerances more directly as this has been shown to outperform surrogate range size measurements in prior studies (58). Finally, diurnal species showed stronger interactions between climate and land-use than nocturnal species, maybe because the highest temperatures organisms experience occur during the day. For our focal species, traits were not correlated (*SI Appendix*, Table S8); thus, the tendency for stronger interactions between land-use and climate for species with a particular trait is unlikely to be a confounding effect of other trait effects. Ultimately, however, the strong community-level patterns indicate that heightened sensitivity to habitat modification in hotter regions may be a general phenomenon among North American mammals.

Limitations. Our study is not without some limitations. First, though studying natural variation across large spatial or temporal scales can indicate important ecological insights when experiments are not feasible (59), our study is nonetheless correlational. It is thus possible that unmeasured factors could drive some of the climate-associated habitat shifts that we observed. For example, our definition of "forest" is broad, and temperature-dependent affiliations with forest could thus reflect changes in species preferences for different forest types along temperature gradients (60). Similarly, if particularly intensive agricultural systems or highly urbanized cities were more likely to occur in hot locations, and diversified farms occurred in cool locations, then species might shift their habitat affiliations to avoid human-dominated habitats in warm locations not because of temperature but rather due to local land-use intensity. Moreover, while we did not detect strong correlations between land-use and climatic variables used in our analyses, forest proportion and maximum temperature showed a weak negative correlation (*SI Appendix*, Table S4). For pumas—the only forest specialist in our analysis whose forest affiliation became significantly stronger with increasing temperature—the tendency of forest habitat to decline with increasing temperature may force individuals into smaller forest patches, thus increasing forest use. However, this mechanism is unlikely to explain the shift—from avoiding to preferring forest as temperature increases—which we observed in most of the species with significant changes in forest affiliation across the maximum temperature gradient. Yet another possibility is that trends could partially result from shifts in species interactions across climate or land-use gradients (61, 62). For example, anthropogenic resource subsidies are thought to increase the spatiotemporal co-occurrence of antagonistically interacting mammals (55). If anthropogenic resource subsidies are more abundant in cooler than warmer regions, then antagonistic species interactions

could force species into natural habitats in warm regions but not cool regions. Second, we limited our analysis to wide-ranging species to ensure sufficient variability in spatial covariates across the species' range; however, narrow-range species may be more specialized compared to species included here (63). Thus, intraspecific variation in habitat preferences may not be as common across a wider swath of North American mammal species as our study suggests. Third, to quantify the effects of traits on climate-dependent habitat preferences, we constructed a rather complex model with multiple random effects alongside two- and three-way interactions. It is possible that the weak trait effects that we observed arose because of model complexity.

Conclusions. While many studies have explored the effects of climate and land-use in isolation, the interactive effects of climate and land-use are less understood but still critical to understanding species distributions (26, 35, 36). Our findings reaffirm that high temperatures may prevent species from exploiting habitats that they might otherwise occupy (64). Looking forward, understanding how and when species track their niches across multiple axes—such as the habitat and climate niches investigated here—will have major implications for elucidating the biogeography of the Anthropocene (65). With ongoing climate change, hot temperature extremes—and as a consequence, maximum temperatures experienced by wildlife—will become even more frequent and extreme (33). Our work suggests these climate extremes may further constrain species distributions and compromise efforts to conserve biodiversity in human-dominated landscapes. More optimistically, however, our results may also provide avenues for developing forward-looking conservation strategies by identifying how human-modified habitats might be managed to provide the microclimatic refugia species need to persist by protecting forests or other cool shady habitats.

Materials and Methods

Camera Trap Data. To study spatial variation in how species space-use is affected by habitat conversion, we used the Snapshot USA dataset, a coordinated survey of camera traps from 196 sampling arrays (different projects contributing data) across the contiguous United States (66, 67). Details on sampling arrays and camera models are reported elsewhere (66, 67). Briefly, sampling arrays were active for a minimum of 400 trap nights (a minimum of ten cameras for at least 40 d and nights). Within an array, cameras were placed 200 to 5,000 m apart from one another, and the entire array was located in one major habitat type (e.g., forest, grassland, etc.). Cameras were positioned 30 to 50 cm off the ground and programmed to take 1 to 10 photographs per trigger. Traps were active from August through November in all lower 48 states in 2019 and 2020. The resulting camera trap data were uploaded to the eMammal Data Management System (emammal.si.edu), and all species identifications were reviewed by at least one expert.

We generated a hexagonal grid across the United States with a diameter of 200 km and centroids separated by approximately 150 km and asked whether species responses to land-cover vary among grid cells or whether they are consistent. To address this question, we filtered the Snapshot USA dataset to only include wild terrestrial mammals with a minimum 350,000 km^2 range size (equivalent to 10 hexagons) within the contiguous United States (68, 69). We opted for large spatial scales to ensure an adequate amount of data in sampled hexagon grid cells. Each species also had to be detected within a minimum of five hexagons. These filtering steps helped ensure that there would be variation in both land-use and climatic conditions across the species' US range, as well as a minimum level of information needed to estimate species associations with these environmental variables. Finally, we only included species that weigh at least 300 g (70), as smaller species are not detected as reliably with the camera trap setup described above and also not as reliably identified (71, 72).

To construct the observation histories, we defined 7 d as one camera trap occasion for which each species could be detected or not. Then, for each site (camera trap location) i, we aggregated binary occasion-specific species detections over all occasions to frequencies; that is, how many times each species k was detected out of the total number of 7-d occasions site i had been surveyed. We did not include any camera traps with active times shorter than seven days. Species observation histories included all sites at which a species was ever detected as well as sites where species were not detected but that were inside the species' geographic range (68, 69).

Covariates. To quantify the association between species' space-use and land-use, we extracted land-cover covariates at a 1-km buffer around each camera site. We determined the forest proportion within each 1-km buffer using the National Land-Cover Database 2016 (73) by summing all pixels categorized as deciduous, coniferous, or mixed forest divided by the total number of pixels comprising the buffer. We determined the anthropogenic impact for each 1-km buffer from the global human modification layer (74). To do so, we used the 30-m resolution human modification map to quantify the average level of human modification across all cells that fell within each 1-km buffer. We also extracted covariates at 5- and 10-km buffers to determine whether or not spatial patterns held at multiple spatial resolutions. Because covariate values were highly correlated across the spatial scales (*SI Appendix*, Table S3), we used the 1-km covariates in model building. To quantify the interacting effects of land-use and climate, we extracted the maximum temperature of the warmest month, minimum temperature of the coldest month, mean annual temperature, and total annual precipitation at each camera trap location from WORLDCLIM, downloaded at a 1-km resolution (75). Total annual precipitation was highly correlated with precipitation in the wettest month and quarter ($r = 0.81$ and 0.84, respectively). We standardized all covariates before model fitting. The range of spatial covariates present within species' US ranges is summarized in *SI Appendix*, Table S2. To quantify how climate-dependent habitat associations change with species traits, we extracted information on species' trophic levels (76), diurnal activities (70), body masses (70), and because of the spatial extent of our analysis, we used range sizes within the continental United States instead of the global range sizes (68, 69) (*SI Appendix*, Table S1).

Model Definition. We used community occupancy models to quantify spatial variation in species' habitat affiliations. Occupancy models use species detections and nondetections from repeated visits to sampled sites to estimate the probability of species occurrence and its relationship with environmental covariates while accounting for imperfect detection (77). Thus, they consist of ecological and observation submodels. Community occupancy models jointly analyze data from multiple species, allowing species-specific and community-level parameter estimates (78). All species-specific parameters are drawn from a common distribution governed by community hyperparameters, allowing estimations for rarer species (79). We built three sets of community occupancy models in a Bayesian framework to quantify whether associations between species' space-use and land-cover are consistent across their US ranges (Set 1), whether climate variables mediate variation in species' responses to land-cover (Set 2), and whether species traits explain the interaction between climate and land-cover (Set 3).

(i) Ecological submodel. We modeled the true occupancy state of species k at site i, z_{ik} (1 if present, and 0 otherwise) as a Bernoulli trial with a probability of occupancy ψ_{ik}:

$$z_{ik} \sim Bernoulli(\psi_{ik}). \qquad [1]$$

Spatial variation in occupancy probability can be modeled as a logit-linear function of covariates c_i:

$$logit(\psi_{ik}) = \beta_{0k} + \beta_{ck}c_i. \qquad [2]$$

Here, β_{0k} are species-specific random intercepts that allow species to vary in their baseline occupancy probabilities. Random intercepts were drawn from a normal distribution, where μ_0 and σ_0 are the community mean and SD.

$$\beta_{0k} \sim Normal(\mu_0, \sigma_0). \qquad [3]$$

Similarly, species-specific effects of covariate c were normally distributed with community hyperparameters:

$$\beta_{ck} \sim Normal(\mu_c, \sigma_c). \qquad [4]$$

Our three model sets included year as a species-specific binary covariate on occupancy probability to account for potential temporal variation. In model set (1), we quantified spatial variability of species' response to land-use by modeling occupancy probability as a function of species-specific land-cover effects. To account for spatial autocorrelation, we included species-specific random effects of sampling array a, ϵ_{ak}, including only arrays within each species' US range and drawing from a normal distribution with SD τ across species.

$$logit(\psi_{ik}) = \beta_{0k} + \beta_{Yk}Year_i + \beta_{Lh_ik}Landcover_i + \epsilon_{ak}. \qquad [5]$$

$$\epsilon_{ak} \sim Normal(0, \tau). \qquad [6]$$

For each species k, the land-cover effect at site i, β_{Lh_ik}, depends on which hexagon h site i is located in. Specifically, we modeled each species' set of β_{Lh_ik} as a normal random effect δ_{Lhk} with SD ω_{Lk}:

$$\beta_{Lh_ik} = \mu_{Lk} + \delta_{Lhk}. \qquad [7]$$

$$\delta_{Lhk} \sim Normal(0, \omega_{Lk}). \qquad [8]$$

We only included hexagons within each species' US range. The species-level intercept μ_{Lk} describes the average response of species k to land-cover L across hexagons and comes from a normal distribution with hyperparameters that are estimated in the model (μ_β, σ_β). The SD ω_{Lk} quantifies the intraspecific variability in species' responses to land-cover across the species' US range. We modeled ω_{Lk} as coming from a shared gamma distribution with hyperparameters a and b:

$$\omega_{Lk} \sim Gamma(a, b). \qquad [9]$$

$$\mu_{Lk} \sim Normal(\mu_\beta, \sigma_\beta). \qquad [10]$$

We classified species as habitat specialists when the β_{Lh_ik} for a given land-cover was either positive or negative for at least 75% of the hexagons within that species' US range and as a generalist for that land-cover otherwise. We used this classification in interpreting the variation in species' responses to land-cover in model set (2).

In model set (2), we quantified how climate affects species' responses to land-use by modeling occupancy probability as a function of climate, land-cover, and their interactions, with species-specific coefficients, and a species-specific random effect of hexagon h, δ'_{hk}, again including only hexagons within a species' US range. Significant interaction effects β_{lk} indicate climate-dependent species associations with land-cover class.

$$logit(\psi_{ik}) = \beta_{0k} + \beta_{Yk}Year_i + \beta_{Lk}Landcover_i + \beta_{Ck}Climate_i$$
$$+ \beta_{Ik}Landcover_iClimate_i + \delta'_{hk}. \qquad [11]$$

In model set (3), we quantified whether species traits affect the interactions between climate and land-use in species space-use. To do so, in addition to the covariates in model set (2), we modeled occupancy probability as a function of a species trait $\beta_T Trait_k$, the interaction of that trait with climate β_{TC}, and land-use β_{TL}, and a three-way interaction between trait, climate, and land-use β_{TCL}. Significant three-way interaction effects indicate a change in the interaction effect between climate and land-use based on a species' trait.

(ii) Observation submodel. Because nondetection of a species at a sampling site can either be caused by a true absence or by a failure to detect, repeated visits over the number of occasions to sampling sites can be used to estimate detection probability p_{ik} conditional on occupancy ($p_{ik} = 0$ where $z_{ik} = 0$, i.e., the species is not present). Observations y_{ik} are assumed to be from a binomial trial, where n_i is the number of sampling occasions at site i.

$$y_{ik} \sim Binomial(p_{ik}z_{ik}, n_i). \qquad [12]$$

Heterogeneity in detection was modeled as a logit-linear function of 1) sampling effort (i.e., the number of days with active camera trapping at site i, X_i) to

account for variation in sampling intensity across sites, 2) species identity α_{0k}, to account for some species being more detectable than others, and 3) a species-specific random effect of sampling array a, ϵ'_{ak}, including only arrays within each species' US range. Sampling array was included to account for potential differences in setup techniques and equipment used by the different projects that contributed data, as well as differences due to habitat in which an array was located, and were drawn from a normal distribution with SD τ' shared across species.

$$logit(p_{ik}) = \alpha_{0k} + \alpha X_i + \epsilon'_{ak}. \quad [13]$$

$$\epsilon'_{ak} \sim Normal(0, \tau'). \quad [14]$$

Species-specific intercepts α_{0k} were drawn from a normal distribution with community parameters:

$$\alpha_{0k} \sim Normal(\theta_0, \tau'_0). \quad [15]$$

Model Run and Diagnostics. We fit the three model sets separately for the two land-use covariates (forest proportion and human modification) for a total of 2, 8, and 8 model runs for model sets 1 to 3, respectively. In model set (2), we combined each land-use with individual climate variables (annual precipitation and minimum, maximum, and mean temperatures). Because of the model complexity, we only included one climate variable and one land-use variable at a time. Similarly, in model set (3), we included one of the four traits at a time, combined with either forest proportion or human modification and maximum temperature. We only implemented models for maximum temperature based on analyses from the model set (2). To ensure our main results are robust to prior choice, we also implemented our models with a potentially less informative Beta(1,1) prior on the community average intercepts for the probability of detection and occupancy and found that parameter estimates were not sensitive to the choice of this prior (*SI Appendix*, Fig. S5). All model definitions are provided in *SI Appendix*.

We used Markov chain Monte Carlo (MCMC) simulation with NIMBLE [version 0.11.1; (80)] in R version 4.0.5 (81) to fit our models. We ran four chains of 200,000 iterations and discarded the first 50,000 samples as burn-in and further thinned the remaining samples by 20. We assessed convergence using the potential scale reduction value for all parameters and by inspecting the mixing of the chains using trace plots (82). We tested whether the model adequately fit the data by calculating a Bayesian P-value (83) (*SI Appendix*, Table S9). We report the posterior mean of all estimates with 90% Bayesian credible intervals (BCI); we interpret coefficients as significant when their 90% BCI does not overlap zero. For SDs (model set 1), we report the posterior mode, because of the expected skewed posterior distributions. Because values of SDs are bounded by zero, we estimated the density using a truncated kernel and evaluated a 90% credible interval using the 90% highest posterior density interval (84). This allowed a value of zero to be included in the 90% credible interval. We used 90% intervals throughout the results to ensure stable posterior densities (85).

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