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Assessing the state of knowledge of contemporary climate change and primates

Andrew B. Bernard[1] | Andrew J. Marshall[1,2,3,4]

[1]Department of Anthropology, University of Michigan, Ann Arbor, Michigan

[2]Department of Ecology & Evolutionary Biology, University of Michigan, Ann Arbor, Michigan

[3]Program in the Environment, University of Michigan, Ann Arbor, Michigan

[4]School for Environment and Sustainability, University of Michigan, Ann Arbor, Michigan

Correspondence
Andrew B. Bernard, Department of Anthropology, University of Michigan, Ann Arbor, MI.
Email: abbernar@umich.edu

Abstract

In recent years, interest in understanding the effects of climate change on species and ecological systems has sharply increased. We quantify and contextualize the current state of knowledge about the effects of contemporary climate change on non-human primates, a taxon of great ecological and anthropological significance. Specifically, we report findings from a systematic literature search designed to assess the allocation of research effort on primates and climate change and consider how the current distribution of knowledge may be influencing our understanding of the topic. We reveal significant phylogenetic and geographic gaps in our knowledge, which is strongly biased towards lemurs, apes, and a relatively small subset of primate range countries. We show that few analyses investigate changes in primate foods relative to changes in primates themselves or their habitats, and observe that few longitudinal datasets are of sufficient duration to detect effects on the generational scale. We end by identifying areas of research inquiry that would advance our theoretical understanding of primate ecology, evolution, and adaptability, and meaningfully contribute to primate conservation.

KEYWORDS
allocation of research effort, climate change, conservation, diet, distributions, habitat, longitudinal data, primates

1 | INTRODUCTION

Since the advent of the Industrial Revolution, human activities have dramatically changed the global climate.[1] Efforts to understand the scope, scale, and consequences of these changes have resulted in a vast "climate change" literature spanning many fields of theoretical and applied science. Here we focus on the subset of this literature that addresses primates: a taxon that is ecologically important, is integral to the field of anthropology, and may be particularly vulnerable to climate change. Our primary goal is to classify and synthesize the body of English language, peer-reviewed research that explicitly investigates how contemporary, largely human-induced climate change has affected, or will affect, non-human primates. We structure this review in three sections. "Climate Change Research" outlines why climate change research is important, highlighting the paucity of work on primates despite their potentially high vulnerability to rapid climate change. In "Current Knowledge" we characterize the distribution of published work, identify specific gaps in our knowledge, consider why those gaps exist, and briefly summarize the relatively small number of published primate studies that explicitly reference climate change. Lastly, "Future Directions" considers how research might progress by posing several key research questions that merit further investigation.

2 | CLIMATE CHANGE RESEARCH

Climate change is defined by the Intergovernmental Panel on Climate Change as a "change in the state of the climate than can be identified (e.g., by using statistical tests) by changes in the mean and/or the variability of its properties, and that persists for an extended period, typically decades or longer" (IPCC,[2] p 126). This definition, when applied to biotic systems, suggests there is an important distinction between climate research and climate change research: the former examines relationships between species and their abiotic environments, and the latter investigates changes in these relationships over time. For the purposes of this review, we consider "climate change research" to be any work that refers to climate change (or global warming) and documents or predicts how the relationship between climate and species changes over time. We focus on climate analyses in the context of changes that have occurred since the Industrial Revolution based on the premise that during this period, humans began unequivocally altering the global climate and rapidly expanded the "anthropogenic biome."[1,3]

2.1 | Why is this research important?

Climate change research is important because it can improve our ability to understand and conserve biodiversity. First, characterizing the effects of contemporary climate change can advance theoretical understanding of key issues in ecology and evolution. For example, studies can elucidate how climate, habitat availability, food availability, biotic interactions, and dispersal combine to influence the geographic ranges of species[4,5] as well as the species richness[6] and structure[7] of ecological communities. Second, research can document how individual species respond to climate change at different rates and shed light on whether ecological communities are best viewed as stable, cohesive units or ephemeral assemblages.[8] Third, climate change research is increasingly critical for species conservation. For instance, understanding climate-species interactions at a mechanistic level permits modeling extinction probabilities under different future scenarios.[9] These and other models can inform conservation strategies to mitigate the effects of climate change, such as the location and design of protected areas[10] that currently may not sufficiently protect vulnerable species from climate change.[11]

2.2 | Climate change research on primates

Knowledge of primates and climate change is growing. The number of primate studies that refer to "climate change" or "global warming" has increased substantially over the last 20 years (Figure S1). Climate change is a key source of environmental stress for primates, especially when combined with other contemporary anthropogenic stressors.[12] Recent global analyses highlight the vulnerability of primates to projected temperature and precipitation changes[13] and extreme weather events.[14] The availability of information about primates clearly lags

behind that of other taxa, however (Figure 1, Box 1). This is concerning, as climate change will likely exacerbate current widespread declines: 75% of primate species are in population decline, and ~60% of primate species are threatened with extinction.[15] Recent large-scale assessments of primate conservation specifically acknowledge our limited grasp on the effects of climate change[15,16] or exclude climate change altogether from discussion of threats to primate populations.[17]

2.3 | Why are primates vulnerable to climate change?

Many primates possess biological attributes, such as dietary generalization and behavioral plasticity, that might superficially lead one to think that they would be relatively unaffected by climate change. In fact, among endotherms primates are disproportionately vulnerable to climate change for several reasons. First, because primates are predominately tropical species that experience relatively mild seasonal fluctuations in temperature, they are adapted to a relatively narrow range of temperatures. This means that they likely live closer to their thermal tolerances than do temperate taxa,[18] increasing their sensitivity to even small changes in temperature. Second, because most primates are non-migratory[19] and occupy stable ranges over time, spatial
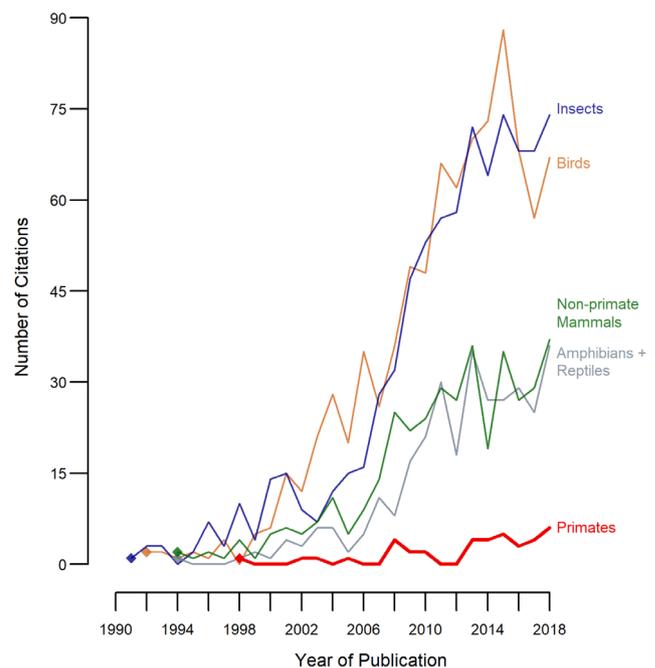
FIGURE 1 Results from a Web of Science literature search (conducted on February 27, 2019) tallying climate change studies by broad taxonomic category. Diamonds indicate the first published study. This figure highlights broad differences in research effort among taxa (see Supporting Information): Climate change studies of birds and insects began earlier and far outnumber those of other taxa. Climate change research on primates began the latest and is the least plentiful [Color figure can be viewed at wileyonlinelibrary.com]

BOX 1 Climate change research on primates versus other taxa

The first peer-reviewed research article that focused specifically on primates and climate change was published in 1998.[109] By that time, the insect climate change literature was sufficiently rich to warrant at least one review article.[110] The corpus of climate change research on non-primate taxa has grown to the point that reviews have been compiled on specific guilds (e.g., herbivorous insects[111]) or geographic regions (e.g., Australian marine mammals[112]). Within the last decade, there have been multiple books (e.g., Møller et al.[113]) specifically addressing the effects of climate change on birds alone. In contrast, the first general review of the effects of climate change on primates was published in 2016,[54] reflecting a general paucity of research attention (Figure 1). Additionally, primates are curiously absent from large-scale studies that focus on species most vulnerable to climate change (e.g., Foden et al.[114]) despite their disproportionate vulnerability.[22]

Why are primates so underrepresented in climate change research? Here we consider two possibilities. First, it may be a simple probabilistic artifact: the Primate clade is less speciose than the other clades depicted in Figure 1. While lower species richness may play a role, primates do not suffer from a general lack of research interest. Known correlates of research effort such as large body size[115] predispose primates to attracting disproportionate attention, and indeed, primates are probably the most well-studied tropical taxon.[29] Thus, it seems unlikely that the relative lack of information about the effects of climate change on primates reflects a lack of available information on primates more generally.

Second, it may be that existing datasets are of insufficient duration to reveal temporal changes in primate populations or detect their responses to altered environmental conditions. Field studies of tropical primates did not begin in earnest until the mid-20th century[72]—much later than research on temperate insects and birds. Perhaps even more crucial, however, are primates' relatively long generation times, especially in comparison to taxa such as insects and birds. Many years of data are required to encompass a single lifespan for most primate species. Primates are also behaviorally flexible, and we may lack datasets of sufficient sample size to establish robust correlations between changes in primates and changes in climate over time.

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movements (e.g., long-range dispersal, migration) that mitigate many other species' exposure to changing environmental conditions (e.g., many birds[20]) are unavailable to them. Primate population movement is further restricted by habitat fragmentation, suggesting that many primates may heavily rely on behavioral flexibility to cope with climate changes.[21] Even if primates were able to shift their ranges, the spatial homogeneity of lowland tropical environments would require populations to move across unrealistically large distances to track changes in their habitats.[22,23] Third, primates' long generation times limit their ability to accumulate beneficial adaptations (i.e., evolve) sufficiently quickly to mitigate the detrimental effects of climate change. These vulnerabilities, coupled with the fact that the ranges inhabited by non-human primates are predicted to experience 10% more warming than the global mean,[13] suggest that climate change is likely to be a major threat to the long-term persistence of many primate species. Indeed, recent climate change has likely already negatively impacted hundreds of primate populations.[24]

3 | CURRENT KNOWLEDGE

3.1 | Literature review

Our objective was to critically analyze the body of work that explicitly links recent changes in climate with the impact of those changes on primates. To compile a database of this research, we systematically searched the English language peer-reviewed literature (including both journal articles and chapters in edited volumes) using three search engines: Web of Science Core Collection, BIOSIS Citation Index, and Zoological Records. Among other restrictions (see Supporting Information for a complete list of search terms), we specifically required studies to include the keywords "climate change" or "global warming." These search terms, and our systematic search method more broadly, were intended to minimize a priori subjective decisions about what constitutes a "climate change" study. We recognize that our search method excluded a broader array of investigations concerning the relationships between primates and their abiotic environment, as well as investigations of climate change and important primate food or habitats that do not specifically mention primates by name (see Supporting Information for further discussion). These excluded studies could certainly further our understanding of the effects of climate change on primates (see Supporting Information for further discussion). Our aim, however, was not to provide a comprehensive overview of these effects, but rather to use transparent decision rules to assemble and comment on the scope of work that explicitly draws connections between changing climate and primates as focal study species.

Our initial search on June 27, 2017 (n = 371 hits) combined with automated email alerts sent to ABB from Web of Science between that date and February 7, 2019 (n = 61) yielded 432 total hits. From this database, we eliminated studies that were not peer-reviewed (n = 30), studies for which the full text was not accessible through the University of Michigan library system (n = 11), and studies for which the article's subject was definitively unrelated to the topic under

investigation (e.g., cases where the search terms were only found in the references, studies about "Macaque" computing software; n = 126). We also excluded all studies written in languages other than English (n = 5); we did not feel we could reliably interpret the context of phrases equivalent to "climate change" in non-English languages, and therefore did not design our query to conduct a comprehensive search of non-English language literature.

We compiled information from the remaining 260 studies in a database (see Table S1 for a full description of the attributes and the Supplemental Spreadsheet for a full list of the studies and the information we collected). Among other attributes, we recorded each study's focal primate species, the country in which the research was conducted, whether the study focused on contemporary or past processes, and whether the study was quantitative or qualitative. Focal primate species were tabulated as individual "records," with one record indicating one focal primate used in one climate analysis; thus, a single analysis could result in multiple records if it specifically addressed multiple species. We defined quantitative climate studies as those that fulfilled three criteria. First, the study used an abiotic climate variable as one of the predictors. Second, the analysis included time as an independent variable. Third, time was represented chronologically, thus excluding studies that analyzed data based on binned times (e.g., Frasier et al.[25]) that did not permit assessment of change over time. We defined a qualitative climate study as one that failed to meet our quantitative criteria but that concretely advanced knowledge of how climate change has or will affect primates (see Table S1). Studies that only referred to climate change in terms of the study's implications (see Supporting Information for how we determined this) were excluded from our analyses. Using these criteria, we scored 188 papers as "contemporary" primate studies, 101 of which incorporated quantitative climate analyses and 74 that presented qualitative discussion of climate change. Fifty-five studies included both.

Because our goal was to identify climate change studies, and climate change inherently occurs over time, our criteria required studies to include a temporal comparison. We did not impose a cutoff for the minimum amount of elapsed time over which data were collected in order to rate studies as including a temporal comparison; a study simply needed to include at least two data points separated in time. While we recognize that most people would assume that climate change studies are necessarily conducted over a period of many years, any cutoff we chose would have been arbitrary and not of equal relevance to all species and regions (see the Supporting Information for further discussion of this point). Still, one could reasonably argue that climate change studies should at minimum incorporate inter-annual variability to account for the highly seasonal intra-annual weather variability experienced by some primates (e.g., many lemurs). To assess whether restricting our analyses to studies that were at least a full year in duration would yield different results, we repeated all analyses with the subset of studies that incorporated at least one elapsed year of cross-sectional or longitudinal data. We include these results in the Supporting Information (Figures S2, S3, S4, S5) but do not discuss them further in the main text, as the results of these analyses were not substantively different from those we obtained using the full dataset.

In the following section, we use this database to identify what is known about primates and climate change and to identify gaps in current knowledge. Specifically, we: (a) assess the distribution of current scholarship as a function of phylogeny and geography; (b) consider the relative amount of information available about climate-related changes in primates, their habitats, and their foods; (c) assess the temporal scope of published observational studies of the effects of climate change on primates; and (d) briefly review current predictions and observed patterns relevant to primate responses to climate change.

3.2 | Phylogenetic and geographic biases

To detect phylogenetic biases in the primate climate change literature, we analyzed the number of records relative to the number of species within a genus. If research effort was equitably allocated and there were no phylogenetic biases, then the records for any given genus should be predicted by the number of species within that genus, resulting in a 1:1 correlation between the number of records and the number of species for each genus. Large positive or negative residual values indicate genera that are disproportionately over- or understudied.

Fifty of the 79 extant primate genera (taxonomy following Estrada et al.[15]) are represented in our primate climate database (Figures 2 and 3). Of these 50 genera, only 18 have more citations than would be predicted if every species in the genus was the focus of one climate change study (Figure 2). Seven species fall exactly on this 1:1 correlation line and 25 species are below the line, indicating that 25 genera are underrepresented in the climate change literature given their diversity. Of these 25 genera, nine (36%) are cercopithecoids (Asian and African monkeys), seven (28%) are platyrrhines (South American monkeys), three (12%) are lorises, three (12%) are lemurs, two (8%) are apes, and one (4%) is a tarsier. These results support prior indications[26] that primate research effort is not equally distributed with respect to phylogeny, and most effort is allocated to a small subset of species.

In particular, there is a bias towards apes and lemurs. Of the six genera with the highest residual values (Figure 2), four are lemurs (*Propithecus*, *Eulemur*, *Microcebus*, and *Cheirogaleus*), and two are apes (*Pan*, *Gorilla*). Of the 18 total genera that are overrepresented given their diversity, 56% (10 genera) are lemurs, and only one lemur genus (*Lepilemur*) comprising more than 10 species is underrepresented given its diversity. Additionally, only apes (14 of 25 species represented) and lemurs (62 of 105 species represented) have more than half of the species in their respective taxonomic groups represented in the climate change literature. Within each of the other four groups, over 80% of their species remain unrepresented in the climate change literature: specifically, studies have focused on 3 of 22 loris species, 24 of 168 platyrrhine species, 29 of 172 cercopithecoid species, and 2 of 11 tarsier species (Figure 3a).
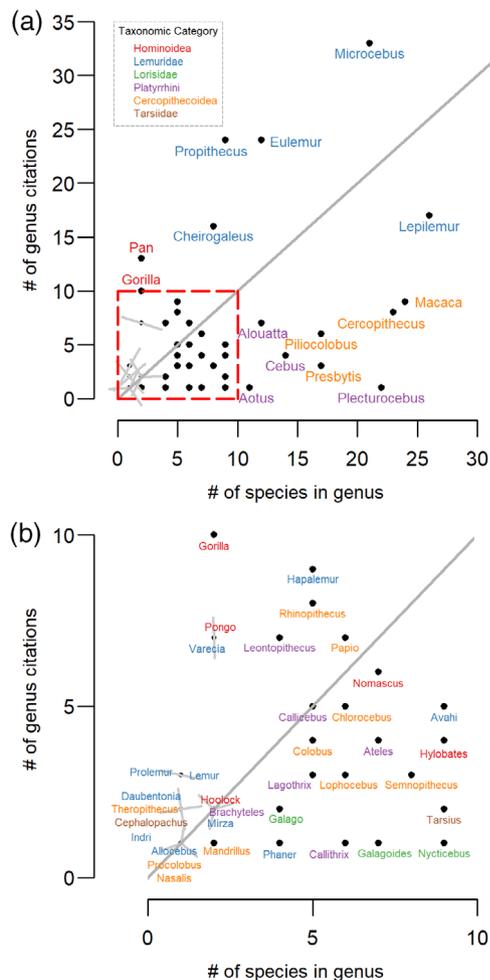
FIGURE 2 Phylogenetic distribution of climate studies (combining quantitative and qualitative research; see Supporting Information) addressing (a) all genera and (b) genera within the 10×10 grid (for visual clarity). The dotted line denotes a 1:1 correlation between the number of species in a genus and the number of climate studies addressing that genus; species under the line are underrepresented given their diversity, and species over the line are overrepresented [Color figure can be viewed at wileyonlinelibrary.com]

Of the six taxonomic groups, cercopithecoids and platyrrhines are the most species-rich, and inequitable effort across these groups with respect to phylogeny is particularly noticeable. Based on their residual values (Figure 2), the five least-represented genera include four cercopithecoids (*Macaca*, *Cercopithecus*, *Presbytis*, and *Piliocolobus*) and one platyrrhine (*Plecturocebus*). Of the 144 unrepresented platyrrhine species, 80 have no represented congener. Similarly, of the 143 unrepresented cercopithecoid species, 50 have no represented congener. Several of these unrepresented genera are particularly species-rich themselves, including *Trachypithecus* (cercopithecoid, 20 species), *Pithecia* (platyrrhine, 16 species), *Mico* (platyrrhine, 13 species), and *Saguinus* (platyrrhine, 12 species).

We also analyzed the number of primate records among all primate range countries and found that climate change studies are unequally distributed with respect to geography. Of the 89 primate range countries, 35 (39%) are represented and 53 are not (Figure 4a). Of the 35 represented countries, seven are only represented once, 29 (83%) are represented five times or fewer, and 31 (89%) have fewer than 40% of that country's species represented (Figure 4b). For each primate range continent (excluding Madagascar from Africa), fewer than 50% of the range countries are represented: specifically, 8 of the 20 primate range countries in the Americas (40%), 15 of 46 range countries in mainland Africa (33%), and 11 of 23 range countries in Asia (48%) are represented. Madagascar has close to an order of magnitude more climate change studies than most other primate-range countries, and accounts for 145 (47%) of the 306 primates addressed by a climate analysis.

Why are apes and lemurs disproportionately represented in the climate change literature? For apes, this may reflect the more general research bias towards this group.[26–28] This bias likely has several underlying reasons, including apes' large body sizes, charisma, or phylogenetic proximity to humans.[29] The bias in favor of work on lemurs is not, however, consistent with broader publication patterns in the primatology literature,[27] and may be in part due to the substantial emphasis on environmental stressors in much early research on this group (e.g., at Beza Mahafaly Reserve[30]). In addition, lemurs have shorter lifespans, increasing the probability that researchers can observe effects of climate change on lemur populations. Among primates, heterothermy, whereby primates modulate their metabolic rate to decrease their energy expenditure, is most common within the Cheirogaleidae family.[31] Climate studies may target these species because the direct influence of climate on their physiological function may increase or decrease their resilience to climate fluctuations depending on their hibernation strategy.[32]

Additionally, lemurs are arguably the most imperiled of all primate taxonomic groups, raising their conservation priority and the corresponding importance of scientific inquiry. Over 80% of lemur species are listed as Threatened (Vulnerable, Endangered, or Critically Endangered) on the IUCN Red List, and 100% of lemur populations are in decline.[15] Among primates, lemur populations are disproportionately exposed to seasonal powerful cyclones[14] that may be intensifying due to climate change,[33] and other threats may interact with climate change synergistically such that lemurs face the most pervasive extinction risk.

The lack of information about many species and regions is concerning. Not only is our current knowledge of the effects of climate change on primates based on a small subset of species that are likely differentially affected by climate change,[24] but many primate populations may already be suffering climate-related declines without our knowledge. Furthermore, a limited number of studies focusing on certain species may not be sufficient to fully understand how traits that increase vulnerability to climate change vary intra-specifically by region or population.[8,24,34] In order to truly understand this variation, fine-grained studies of responses to local conditions are prudent, especially given that isolated populations are more vulnerable to extinction.[35]

Because ecological traits are not evenly distributed across the primate phylogeny, taxonomic gaps in knowledge may produce holes in
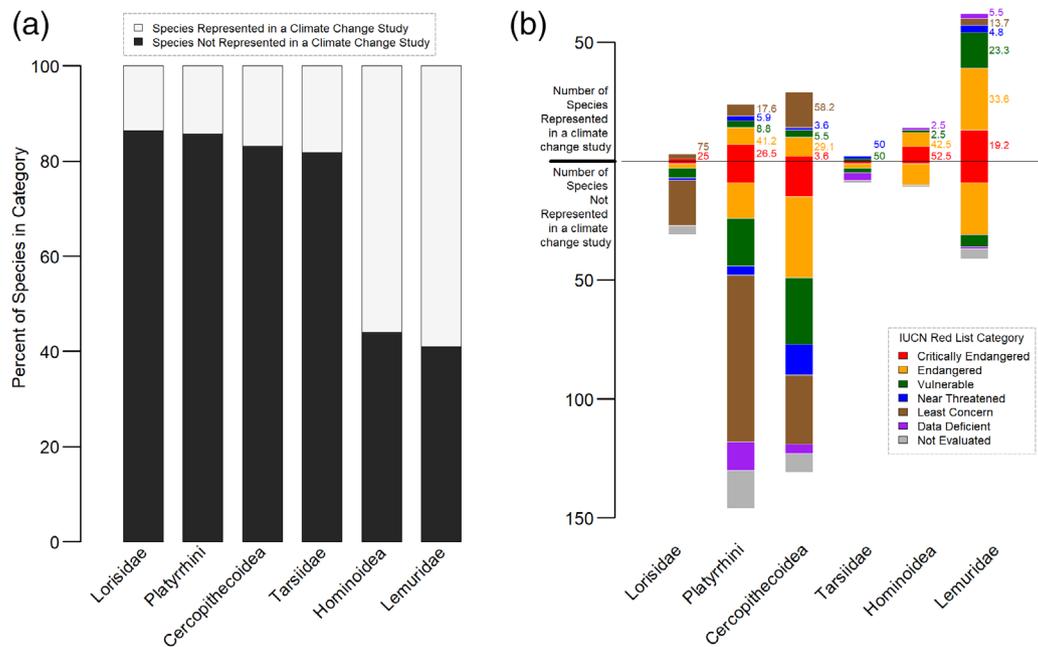
FIGURE 3 Taxonomic diversity of primates in climate studies. (a) Percent of species represented and unrepresented in our database. Bars are ordered left to right by increasing percentage of species represented. (b) Bar height indicates counts of represented (above horizontal line) and unrepresented (below horizontal line) species in climate studies. Bar segments separate counts by IUCN Red List categories. Numbers next to segments indicate the percent of records for each IUCN category. A "record" indicates one focal primate used in one climate analysis (a single analysis can include multiple records). For example, of the three species of Loris in our database, two are Least Concern and one is Critically Endangered. Seventy-five percent of Loris analyses are conducted using the two Least Concern species, and 25% of Loris analyses are conducted using the one Critically Endangered species [Color figure can be viewed at wileyonlinelibrary.com]

our ecological knowledge as well. We analyzed the residual values from the distribution of genera in Figure 2, and did not find systematic biases among genera with respect to body size, percent frugivory, or group size (Figure S6). However, holes in our ecological knowledge still exist. With 82% of tarsier species unrepresented, for example, we know very little about how insectivorous species may respond to climate changes. Additionally, because certain geographic regions are underrepresented, we lack knowledge of certain forest types and seasonality patterns. For instance, much more is known about climate change responses in the highly seasonal wet forests of Madagascar compared to the aseasonal mast-fruiting forests of Southeast Asia, where climate change will likely have distinct effects.

Species known to be most susceptible to other threats are also underrepresented in the climate change literature. Of the 90 Threatened cercopithecoid species (Estrada et al.[15]), only 13 (or 14%) are represented in the database (Figure 3b). Lorises (1 of 7: 14%), platyrrhines (17 of 61: 28%), and tarsiers (1 of 6: 17%) also have low percentages of Threatened species represented. Apes (13 of 23, or 57%) and lemurs (54 of 90, or 60%) are the only taxonomic groups for which Threatened species are more likely than not to be represented.

Of particular concern are the unrepresented species also predicted to be exposed to the greatest magnitude of temperature and precipitation changes. In a global-scale evaluation of primate vulnerability to climate change, Graham and colleagues[13] identified nine such primates. Five of these highly vulnerable species (*Alouatta arctoidea*, *Galago gallarum*, *Semnopithicus ajax*, *Semnopithecus hector*,

Semnopithecus schistaceus) are unrepresented in climate change studies, and the remaining four (*Alouatta pigra*, *Alouatta geoffroyi*, *Cercocebus galeritus*, and *Macaca sylvanus*) are the subject of just three climate change studies combined.[36–38]

3.3 | Primates, habitat, and food

Studies that further our knowledge of primates and climate change extend beyond direct associations between climate and primates themselves. Because primates do not live in isolation in their environments, we also need to consider broader community-scale perspectives.[39] To interpret these broader patterns, here we examine the direct impacts of climate change not just on primates themselves, but also on primate foods and habitats. To quantify our relative knowledge of the direct impacts of climate change on primates, their habitat, and their food, we grouped quantitative climate studies into three categories based on the dependent variables addressed: properties of (a) primates themselves (e.g., physiological tolerance, social behavior, demography), (b) primate habitats (e.g., habitat suitability, forest connectivity), and (c) primate foods (e.g., quality, phenology, availability). While food is an important part of the resource base that defines a habitat,[40] we recognize food and habitat as distinct categories: food is not the sole factor that influences where a primate can live, but is itself a primary determinant of habitat quality and often limits primate population density.[41] Further, we do not incorporate food availability

FIGURE 4 (a) Number of focal primate records and (b) percentage of resident species in climate studies, by country. We note that mainland France appears to be designated as a range country only due to its association with French Guiana, where primates do live [Color figure can be viewed at wileyonlinelibrary.com]
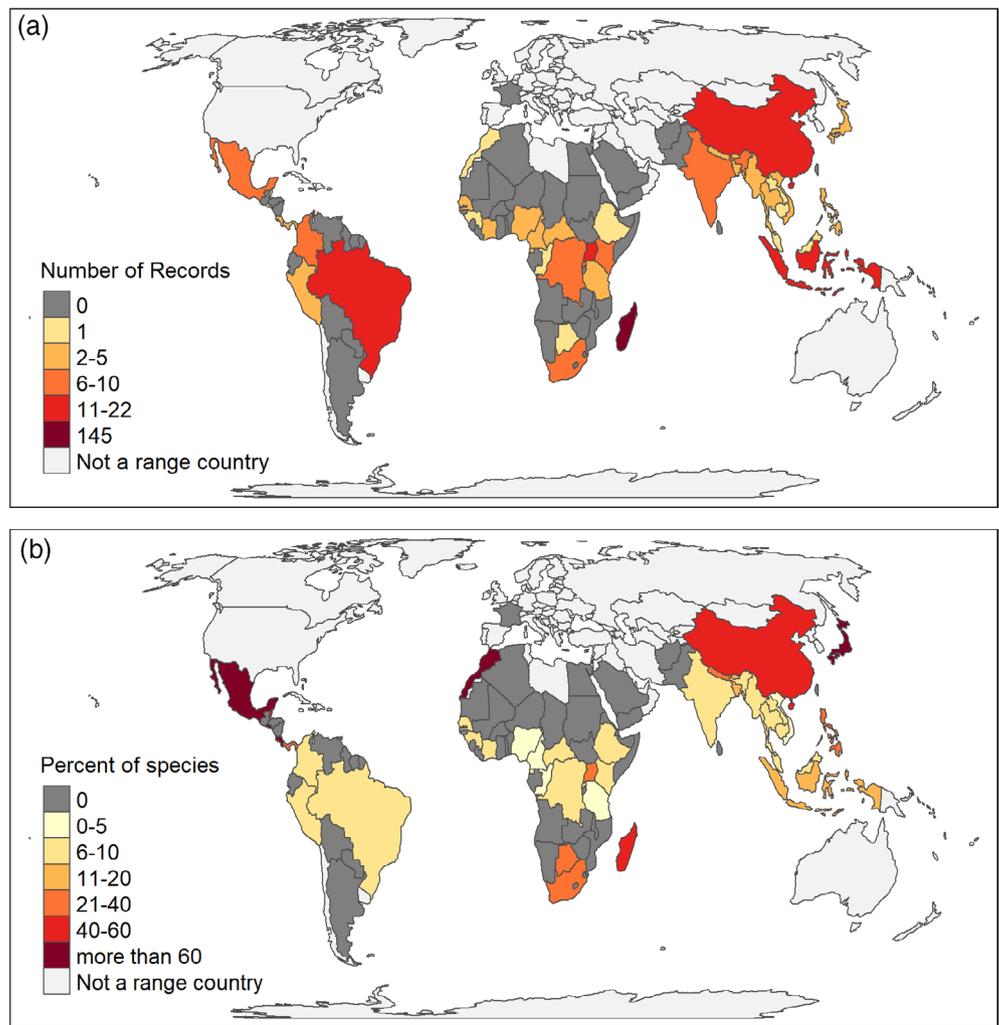
within "habitat suitability," a term we employ to reflect only the attributes commonly used to predict species' distributions: bioclimatic, landcover, topographic, and human impact variables (e.g., sensu Luo et al.[42]).

We specify these three variable classes for two primary reasons. First, the impacts of climate change on primates may be mediated through effects on their habitat and food resources,[43] and it is important to assess how climate change may differentially affect these elements.[44] We recognize that there is substantial breadth of dependent variables within each category (e.g., "primate variables" encapsulates physiology, behavior, demography, ecology, etc.) however we designed these categories only to permit broad ecological comparisons. Second, ecological communities likely do not shift as tightly-linked assemblages, and assumptions about generalized community-level patterns along elevational gradients (e.g., lowland forests "shifting upslope") may be oversimplifications. On the contrary, habitat changes can precede—and ultimately drive—evolutionary responses in the species within them.[40] By distilling communities into distinct functional parts, we are better situated to understand the persistence of novel species assemblages formed by divergent species' responses to climate change,[8] as well as interpret the

different timescales on which species respond. For example, while plants are more likely to migrate than adapt in place,[45] primates may more readily change their behavior in place given their dispersal restrictions[22] and propensity for inter- and intraspecific behavioral variation.

Overall, analyses of changes in food are the least common, while primate analyses are the most common (176 records within primate analyses, 55 records within food analyses, and 151 records within habitat analyses). This is likely at least in part because our primate dependent variable category was much broader than the food or habitat categories. Primate variables included attributes of primate populations and distribution, demography (sex and age class ratios, birth rate, birth season, fecundity, mortality), behavior (activity budgets, food choice and consumption), and metabolic function (body size, energy expenditure, body temperature, metabolic rate, torpor duration, parasite load, tooth size, metabolic biomarkers). Most food variables provided indices of availability (proportion of fruiting trees, fruit productivity, fruiting tree density), and a few indicated the distribution of fruiting trees and indices of food quality (available energy, protein: fiber ratios). The vast majority of habitat analyses measured or predicted changes in habitat suitability, although several studies

analyzed vegetation structure (e.g., tree height, stem density), projected vegetation/forest cover, or assessed forest connectivity.

Given the importance of food in primate ecology and evolutionary biology (e.g., Marshall & Wrangham[46]) the paucity of food-specific analyses in the primate climate change literature is puzzling. Admittedly, food analyses are likely underrepresented in this review because of our choice of search terms (see Supporting Information). For example, analyses that assessed changes in primate foods but did not mention the terms "climate change" or "global warming" would have been excluded. Additional factors may also contribute to this result, however—notably, the scarcity of long-term datasets on tropical plant phenology. Our knowledge of primate foods and climate change, however, may not be as limited as the paucity of food-specific climate analyses may seem to indicate, and insights into primate food are certainly embedded within other variable classes. For instance, an analysis of edge effects on tree species in Bwindi Impenetrable Forest, Uganda[47] almost certainly incorporated species central to primate nutrition, although the dependent variables used in analyses (e.g., "distance from edge") were habitat variables.

Although food is rarely a focal outcome variable in our database, it is a key predictor in multiple analyses of relevance to understanding climate change. For example, Behie and colleagues[48] found that change in fruit consumption over a 5-year period was the best predictor for the population density of Black Howler monkeys (*Alouatta pigra*) following an extreme weather event, and Canale et al.[49] experimentally modified food availability to test the resilience of gray mouse lemurs (*Microcebus murinus*) to food shortages. These studies, though not designed to investigate patterns in food availability itself, do shed light on the significance of food to primate populations in the context of environmental change.

Inclusion of multiple types of predictors can buttress correlations between climatic and biological variables. For example, changes in food abundance over time may be more biologically meaningful when interpreted in the context of the primate social dynamics that also likely affect access to food. Increasingly, studies are incorporating a multivariate approach that explicitly acknowledges community interconnectedness and climate change's cascading effects. We note several examples: Johnson and colleagues[50] compared how both primate density and forest structure responded to a cyclone, and multiple studies[36,51] have generated distinct species distribution models for primates and their important food trees. Raghunathan and colleagues[52] also investigated changes in food and habitat by modeling the future distribution of important food and sleeping tree species for two *Leontopithecus* species.
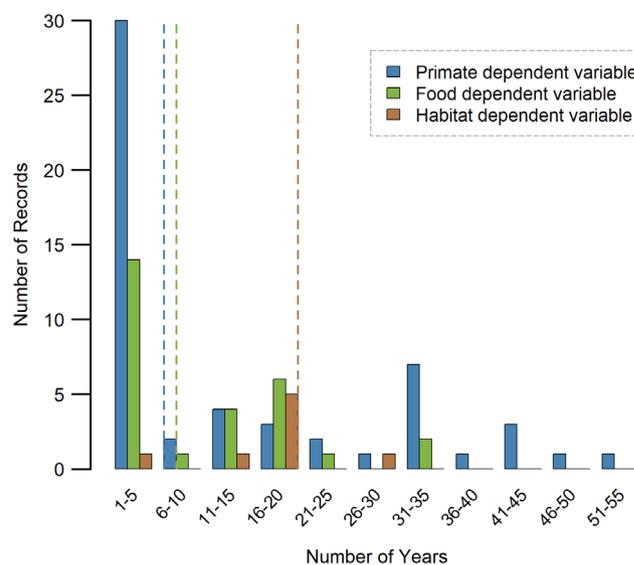
3.4 | Time series data

Many key questions regarding the effects of climate change on primates can only be answered by long-term, observational study, and we sought to quantify the extent to which long-term datasets have been applied to climate change research. We found that few studies in our database use time series data, and most that do are relatively

short-term. Although short-time series may yield valuable information, longer-term studies are more likely to advance understanding of the effects of climate change on primates—both because they may provide a stronger signal of biologically meaningful change and because they permit use of models that can differentiate and explicitly identify secular trends, seasonal variation, and random noise. These considerations are especially pertinent for long-lived species such as primates, for which few datasets span even a single generation.

While habitat is not the least frequent of the three dependent variables within our database, time series analyses of habitat variables are the least common. Time series studies of primate variables are the most abundant (54 records) and have the broadest range, from <1 year to almost 52 years, with a median of 5 ± 15.7 years (Figure 5). The 27 records of food analyses range from less than 1 year to 35 years, with a median of 6 ± 10.5 years. The eight records of primate habitat analyses range from five to 26 years, with a median of 20 ± 6 years. Thus, our current understanding of habitat change is predominately based on projections rather than observed shifts through time. Furthermore, studies presenting long time series come from a small number of sites, with particularly numerous contributions from Kibale National Park.

Analyses have also employed an array of data collection methods that varied in their sampling intensity and consistency. Roughly 50% of studies did not maintain a continuous, consistent sampling regime for their duration, or were snapshot comparisons by design; Chapman and colleagues,[53] for example, compared individual cercopithecine parasite loads in 1974 and 2008 using discrete datasets from each of those years. Such cross-sectional (rather than longitudinal)

FIGURE 5 Frequency distribution of time series data used in quantitative climate studies. Vertical dotted lines indicate the median number of years for each variable type (e.g., the blue line shows the median duration of time series datasets using primate dependent variables). These data are from observational studies only and exclude temporal analyses that project into the past or the future. "Number of years" represents elapsed time between beginning and end of data collection, regardless of sampling regime [Color figure can be viewed at wileyonlinelibrary.com]

comparisons may suggest changes over time, but generally do not permit robust extrapolation of the results into temporal trends.

3.5 | Predictions and patterns

Thus far we have quantitatively assessed our knowledge of primates and climate change and discussed potential explanations for why gaps in our knowledge may exist. Below, we briefly summarize the descriptive results of this research. We do not comprehensively review knowledge of the effects of climate change on primates more broadly, as other recent studies have done this.[21,54] Rather, we highlight patterns that have emerged from studies that draw explicit links between contemporary climate change and primates, their food, and their habitats.

Predictions about the effects of climate change on primates vary considerably. Range shift forecasts exemplify this variation: while many models predict that the extent of suitable primate habitat will decrease, studies that incorporate multiple species often reveal contrasting projections for those species. For instance, Brown & Yoder[55] modeled the distribution of 57 lemur species, and predicted that 60% will experience range reductions, 16% will expand their ranges, and 23% will experience no range changes by 2080. Within a single species, predictions of habitat suitability can vary among populations, and one population's habitat may remain stable while another's becomes completely unsuitable (chimpanzees [*Pan troglodytes ellioti*][56]). Similarly, predictions of changes in habitat suitability can differ dramatically among protected areas currently inhabited by large primate populations.[57]

No study in our database reported a contemporary range shift in primates in response to climate change. Grueter and colleagues[58] did observe that food species frequently consumed by mountain gorillas (*Gorilla beringei beringei*) had undergone elevational shifts over 21 years, but did not investigate changes in the gorillas themselves in response to the shifts in their food resources. Instead, range shift analyses are based on predictive models that forecast changes in future (or past) habitat suitability along altitudinal and latitudinal gradients. For example, Luo and colleagues[42] predicted that by 2020 the range of golden snub-nose monkeys (*Rhinopithecus roxellana*) would decrease by 30% and their median altitudinal range would increase by more than 100 m. More distant projections for 2070–2080 often predict more severe population reductions surpassing 80% (e.g., snub-nose monkeys,[42] lion tamarins [*Leontopithecus* spp.][57]) and even complete extirpation (Hoolock gibbons [*Hoolock hoolock*][59]).

Many studies have demonstrated that primates are affected by relatively short-term temporal changes in abiotic conditions at both local and regional scales (e.g., fertility[60]; offspring sex ratio[61]). Such changes (e.g., rising temperatures, more severe droughts) are often deleterious for primates, resulting in lower birth rates (northern muriquis [*Brachyteles hypoxanthus*][62]), declines in reproductive output (white-faced capuchins [*Cebus capucinus*][63]), or increased offspring mortality[63]). These results indicate that climate change will likely threaten many populations' persistence.[62]

Empirical results indicate that increasingly dry conditions may be particularly problematic for primates. Food production tends to be lower in the dry season.[64,65] Arid conditions can also decrease food quality resulting in reductions in individual health and lower population densities (gray-brown mouse lemurs [*Microcebus griseorufus*][66]), although increased rainfall seasonality has also been shown to correlate with increased leaf quality.[67] More severe droughts and longer dry seasons also lead to decreased reproduction (northern muriquis and brown woolly monkeys [*Lagothrix lagotricha*][62]). Longer dry seasons may also be energetically challenging: for example, greater bamboo lemurs (*Prolemur simus*) almost exclusively feed on bamboo culm in the dry season, a food source that may not sufficiently sustain lemur populations as dry seasons get longer.[68]

Some primates may have evolved the capacity to buffer themselves against the deleterious effects of rapid environmental changes. Strategies to accomplish this include behavioral flexibility, heterothermy, and demographic buffering (a process in which the variation of life history traits most influential for population growth remains low[60]). These evolved strategies may allow primates to persist under unpredictable environmental conditions[50] and during periods of negative energy balance.[69] It is unclear, however, to what extent these adaptations will remain effective in increasingly fragmented landscapes where populations are more vulnerable to stochastic events, genetic isolation, and the loss of adaptive genetic diversity or specific adaptive alleles due to genetic drift.[70]

Overall, our knowledge of the effects of climate change on primates is dominated by short-term observations and predictive models of a limited subset of species, and the relatively small body of work often reports equivocal results. Even fundamental traits such as survivorship are not consistently correlated with changes in climate.[60] Similarly, primates may not be universally sensitive to extreme weather events: while a typhoon decreased the population density of Philippine tarsiers (*Carlito syrichta*) by 81%,[71] Gray-headed lemur (*Eulemur cinereiceps*) abundance was similar before and after a cyclone.[50] This inconsistency is unsurprising, given that climate changes themselves will differ among regions,[13] and precludes formulation of blanket predictions about primate sensitivity and responses to climate change. Fortunately, we are well-positioned to substantially improve our understanding in the coming decade. Primates are an unusually well-studied tropical taxon,[26] and their extensive intra- and inter-specific variability make them ideal focal species for ecological and anthropological study. The dawn of long-term primate field research was the mid-20th century[72] and researchers can therefore apply robust 50+ year longitudinal datasets to investigate changes through time in an increasing number of primate species.

4 | FUTURE DIRECTIONS

Our knowledge of the effects of climate on primates is growing, but is still rather restricted with respect to phylogeny and geography. Due in part to these knowledge gaps, our ability to detect and predict biological responses to climate change is still quite limited. More generally,

however, the effects of climate change on ecological systems can be complex[73]: in order for methods that describe and predict these effects to be tractable, researchers commonly employ approaches that overlook biological factors that are likely to be important (e.g., biotic interactions, the evolutionary adaptiveness of individual lineages, adaptations of ecosystems themselves[74]). Emerging methods are beginning to incorporate such factors (e.g., to predict range shifts[75]) and will likely substantially improve the accuracy and biological realism of climate change studies.

Below, we outline eight outstanding questions that we believe ongoing and future work could profitably address. Answering these questions would advance our theoretical understanding of primate ecology, evolution, and adaptability, and meaningfully contribute to primate conservation.

4.1 | How is climate change affecting primate habitats?

While habitat loss is commonly cited as a primary human-induced threat to primate populations, research rarely implicates climate as a driver of observed habitat loss. Rather, of the studies in our database that analyze habitat dependent variables, almost all (103 of 121 records) employ species distribution models to predict changes in suitable primate habitat. Further, the majority of these records (77%) employ Maximum Entropy software (Figure S7). It is potentially concerning that we derive the most knowledge surrounding climate-induced habitat change from these predictive models: they are subject to frequent misuse,[76,77] can be strongly impacted by sampling bias,[78] and often conflate fundamental and realized niches by failing to incorporate biotic interactions into species' ranges.[79] To the greatest extent possible, it is imperative that these models incorporate biogeographical and ecological attributes of species[76] in conjunction with broadened efforts to investigate observed habitat changes that may be attributable to climate.

4.2 | How is climate change affecting functional aspects of food?

Very few studies in our database specifically investigate trends in primate food sources, and of those that do, most focus on frequently consumed food species[52,58] through observations of fruiting tree behavior.[64] These patterns indicate more broadly a paucity of work that combines food-specific analyses with explicit references to climate change. While such investigations are essential, focusing on the phenology of commonly eaten plants might miss ecologically crucial trends. For example, as patterns of food availability shift with climate change, primates may experience longer or more extreme periods of nutritional stress. As a result, it is important to increase our focus on both the nutritional quality and availability of resources that primates rely on when commonly eaten or preferred foods are scarce.[46] Leaves in particular may emerge as a research focal point as a primary dietary item for folivores and an important fallback food for many frugivores.[46] Recent studies that examine changes in nutrient composition of primate foods and leaf quality over time[65,80] provide valuable models for how knowledge may be advanced in this area.

4.3 | How accurate are current predictions of range shifts?

We will soon be able to assess the accuracy of the forecasts made by species distribution models, some of which predict detectable range shifts as soon as 2020 (e.g., Luo et al.,[42] Ramos-Fernández et al.[36]). Assessing model accuracy will allow us to validate (or not) empirical projections, permit model calibration, and evaluate the biological reality of the method's underlying assumptions.

These assessments are critical because model outputs are highly contingent on their underlying assumptions and initial parameters. For example, "standard" correlative models using 18 climatic predictor variables suggested that by 2090 there would be no suitable habitat left for the mountain gorilla within the protected areas it currently inhabits, whereas a "limiting-factor" model that uses a proxy of primary productivity suggested that climate suitability would remain fairly stable.[77] Comparing the short-term accuracy of models built using different initial parameters will allow us to assess which initial values produce the most reliable predictions and refine our projections.

Our confidence in model projections declines as we make predictions about the more distant future; thus, assessing the accuracy of model predictions for the near future in particular (for which we have the least uncertainty) will be telling. If we learn that our models lack predictive power in the short-term, we will need to consider why. It is possible that range shift models will fail to be useful because they do not incorporate meaningful variation in population processes across a species' geographic range. If this is the case, we may improve their predictive power by incorporating recent methodological advancements to assess and classify range shifts that account for spatial variation in population and demographic processes (e.g., source/sink dynamics, proximity to range boundary[75]). It could also be that models fail to accurately predict changes because future climates may have no modern analogues.[81]

4.4 | How do trends vary within species and across space?

Increasing evidence suggests that species' responses and vulnerabilities to climate change are influenced by species-specific traits.[24] For example, even when multiple primate species share the same habitat, species respond to environmental change differently.[51] Recent research suggests that traits vary substantially across species' ranges,[82] and species' responses may vary in part due to the strong influence of local weather conditions.[60] This suggests that species' traits exist in a complex interplay with "region-specific" factors,[34] and

that predictions of primate responses to climate change are most likely to be useful at the population-specific level. Several primate species, such as chimpanzees, have been studied at many locations for multiple decades[83] and may provide a valuable opportunity to examine intraspecific differences through time.

It is unrealistic to advocate for research programs to target every population of each primate species. Indeed, assuming that every individual population has a distinctive response to climate change may indicate a lack of our understanding of climate responses rather than true heterogeneity. In 1995, Lawton[84] proposed that climate responses may be organized into "functional groups," such that differences within the groups are smaller than those between groups. If it could be done in a robust manner, achieving this functional standardization—whether by taxonomy, geography, habitat, dietary regime, behavior, and so forth.—may greatly accelerate our ability to predict and assess primate responses to climate change. As a starting point, we might draw from comparative biogeography studies and look to establish functional groups in Africa, Madagascar, and the Neotropics where rainfall predicts primate community structure.[85]

4.5 | What role will behavioral plasticity play?

The ability of primates to disperse to track changes in their habitat is limited,[22,23] and most may rely on phenotypic plasticity or novel adaptations to avoid extirpation (although populations occupying an altitudinal gradient may be an exception). Unfortunately, although there is a rich literature on primate behavior in general, we lack robust correlations between primate behavior and climate change. Indeed, there is a paucity of climate change studies that investigate behavioral change in general.[86] Among primates, the magnitude of behavioral responses will likely vary considerably. Current projections based on models of enforced resting time suggest that apes will not be able to successfully adapt in place,[87] and the scope of primates' flexibility itself may be progressively constrained by increases in temperature (vervet monkeys [*Chlorocebus pygerythrus*][88]). However, many primates are dietary generalists, an attribute that may well buffer them against potential changes to the variety and quality of their food. Additional investigations will shed light on the magnitude of behavioral responses to changing climate, and the extent to which behavioral flexibility will enable primates to adapt to rapidly changing environments. In particular, the field would benefit from long-term studies explicitly designed to investigate primate behavioral change and the drivers of those changes.[21]

4.6 | How does climate change interact with other threats?

Climate change will likely exacerbate the negative consequences of other human-induced environmental stressors.[12] For example, habitat fragmentation restricts genetic diversity and may therefore limit primates' ability to evolve in response to rapid environmental change.[89]

Climate change is also likely to influence rates of disease transmission and pathogen outbreaks fueled by warmer temperatures may accelerate population declines more rapidly than otherwise anticipated.[35] Climate-induced changes in agricultural production or prey densities might also intensify the risks primates face due to human subsistence hunting.

Threats to primate populations do not operate in isolation, and accounting for interactions among threats in predictive models is a substantial and challenging task for future climate change research. Multiple effects can be incorporated into a single model either additively, where the outcome's magnitude is the sum of the independent factors, or synergistically, where independent factors interact and magnify each other's effects.[90] Synergistic models in particular are rare in the climate change literature, but the few studies to date predict that interactions between multiple factors have a greater impact on species' physiology and behavior than would climate alone.[90] For this reason, we should strive to characterize such interactions where they occur, as failure to do so may limit the efficacy of conservation management strategies.[91]

4.7 | What are the direct links between primate physiology and climate change?

While there is a foundation of work that investigates how external factors such as temperature, precipitation, and food availability influence primate physiology,[31,92] fewer studies focus specifically on direct links between primate physiology and climate change. There are, however, good reasons to expect that climate change will have direct physiological effects, especially for small-bodied primates.[93] Multiple primate species modulate their metabolism and energetic expenditure based on external temperatures,[31] and research on other mammalian species such as flying foxes (*Pteropus* spp.) has shown that extreme climatic conditions have devastating effects when a certain temperature threshold is crossed.[94] Extreme temperatures could be physiologically detrimental to primates as well, as indicated by a laboratory study of squirrel monkeys (*Saimiri sciureus*) in which individuals experienced extreme heat stress at temperatures in excess of 36°C.[95] We suggest further (nonexperimental) investigations of the role of thermoregulatory stress as an evolutionary challenge across primate taxa, including large-bodied homeothermic species (e.g., chimpanzees[69]), as well as analyses that strive to incorporate primate physiology into mechanistic climate change models.[93]

4.8 | How long are the time lags between exposure and response to climate change?

Time lags temporally separate a species' response from the environmental change that induced it. Although time lags are known to vary considerably in duration among communities[96] and broadly between animals and plants,[97] we lack an in-depth understanding of how time lags may vary both inter- and intra-specifically. Interspecific variation

is likely because species traits (e.g., life history) differentially impact species' sensitivity to climate. Time lags could also vary within species: climate may disproportionately influence individuals at certain critical stages of their life cycle,[98] and therefore the rate at which individuals react to changes in climate.

It is possible that sufficient environmental change has already occurred to incite population responses, but not enough time has passed for us to observe them. Populations may currently occupy unsuitable habitats, bearing yet unobserved "extinction debts"[99] that will result in deterministic population declines. An enriched understanding of time lags will allow us to better perceive these impending responses, as well as predict the time frame of future responses as climate continues to change.

GLOSSARY

Adaptiveness of individual lineages: How the evolutionary history of a lineage results in traits that are advantageous or disadvantageous for descendant populations of that lineage (e.g., to manage rapid climate changes).

Biotic interactions: Also known as species interactions; interactions among organisms (e.g., predation, competition, mutualism), in contrast with organisms interacting with their abiotic environment (e.g., temperature, precipitation, nutrient availability).[1,100]

Extinction debt: "In single species, the number or proportion of populations expected to eventually become extinct after habitat change."[101] As it applies to climate change, the range a population occupies may no longer climatically suitable, resulting in deterministic population declines.[99]

Heterothermy: A behavioral strategy common to mammals, but rare in primates, wherein individuals use torpor or hibernation to modulate their metabolic rate and decrease their energy expenditure.[31]

Intraspecific behavioral flexibility: Variability in behavior within a species at the individual, group, or population level that may or may not have adaptive value.[102]

Longitudinal data: Data collected on a focal variable (e.g., individuals, groups, populations, climate metrics) systematically over time.

Long-term phenological data: Longitudinal phenology datasets, for example, the fruiting behavior of trees, collected over intervals long enough to permit robust investigations of interannual changes in fruiting patterns over time, as well as the drivers of those changes.[103,104]

Maximum Entropy (MaxEnt): A popular but widely scrutinized tool to model the potential current distribution of species. MaxEnt models also predict how species distributions may be influenced by ecosystem drivers such as land use change and climate change.[78,105]

Range shift: Species or populations shift their geographic range in response to a change in the environment, land use, or management regimes.[106] Climate-induced shifts habitually occur across latitude or elevation gradients.[107]

Synergistic interactions: A multiplicative (rather than additive) interaction between variables such that the effect of one can exacerbate the effect of the other, such as climate change and land use change.[108]

Time series: Any time-ordered sequence of observations. Time series can be analyzed based on characteristics of the observed data (time series models) or used to project future values (time series forecasting).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the Supporting Information published online.

ORCID

Andrew B. Bernard https://orcid.org/0000-0001-7205-0187

Andrew J. Marshall https://orcid.org/0000-0002-7703-8811

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AUTHOR BIOGRAPHIES

Andrew B. Bernard is a PhD Candidate in Anthropology at the University of Michigan. He has broad interests in primatology, climate biology, and conservation biology, and currently carries out fieldwork on primates and their food at Gunung Palung National Park, Indonesia.

Andrew J. Marshall is a Professor at the University of Michigan. He is interested in the ecology and conservation of vertebrates and tropical forests, and for more than two decades has conducted research, conservation, and capacity building activities in Indonesia.

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