Primate Distribution Dynamics and the Effects of Contemporary Climate Change Along an Elevational Gradient in Indonesian Borneo

by

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Dedication

To KJB, BRB, AEB, AZ, and NH,

with whom I'm always home.

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Abstract

Climate is a major driver of global change and can force both gradual and abrupt environmental transitions that profoundly influence traits of organisms, the quality of their habitats, and the persistence of populations. In an age when humans are drastically altering global patterns of temperature and precipitation, field studies of extant species are crucial to generate predictions about the future of modern populations, as well as grasp the ecological foundations underlying differential evolved species' responses to climatic change. To that end, interest in how climate change affects modern species and ecosystems is surging, and studies of diverse taxa have shown that most species respond by either shifting their ranges or altering their behaviors. However, investigations of primates and their evolved response mechanisms remain rare and challenging, in part due to their slow life histories and fragmented habitats that may impede their potential to disperse.

This dissertation addresses these gaps by summarizing the state of knowledge of nonhuman primates and the effects of contemporary climate change, followed by two studies that consider whether climate change may drive nonhuman primates to shift their distributions along a continuous elevational gradient at the Cabang Panti Research Station in Gunung Palung National Park, Indonesian Borneo. At Cabang Panti, decades of data have been collected on weather, food availability, and the abundance of five diurnal primate species: Western Bornean orangutans (*Pongo pygmaeus wurmbii*), White-bearded gibbons (*Hylobates albibarbis*), Red leaf

monkeys (*Presbytis rubicunda*), Long-tailed macaques (*Macaca fascicularis*), and Pig-tailed macaques (*Macaca nemestrina*).

For all primates except pig-tailed macaques, abundance of individuals declined over 35 years and withdrew from certain lowland forests disproportionately relative to upland forests. Upward distribution leans (i.e. relative abundance increases towards the uphill range limit, and relative decreases at the downhill range limit) were also evident for orangutans and gibbons as relative counts increased in upland forests. Maximum temperature was not strongly related to counts for any species. Minimum temperature, precipitation, and food availability were not strong predictors of overall trends in primate abundance but were reliably associated with counts at certain elevations. Weather conditions themselves at Gunung Palung were not consistent with broader regional patterns. Over the last 15 years, Cabang Panti has gotten cooler and wetter while Borneo generally trends hotter and drier. Collectively, these results provide key insights into the diversity of ecological parameters that can influence primate behavior in a heterogeneous landscape, and thus the importance of accounting for both species' abiotic and biotic environments in projections of future change. These findings also reinforce the significance of elevation gradients in an evolutionary context as potential climate refugia for primates and other tropical vertebrates.

Chapter 1: Introduction

1.1 Background

Identifying the factors that impact a species' range and behavior is a fundamental area of interest in evolutionary biology, anthropology, ecology, and conservation (Holt, 2003). For example, evolutionary anthropologists seek to reconstruct the abiotic and biotic environments in which primates generally and hominins specifically evolved, and how these ecological conditions changed through time (Kingston, 2007). Conservation of modern species also depends on our ability to determine populations' vulnerability to ecological change, and how ecological factors regulate their environments as dynamic ecosystems.

Climate is a major driver of environmental change on both ecological and evolutionary scales. Climate change can force both gradual (Bennett, 1990) and abrupt (Alley et al., 2003) transitions that can induce high rates of biotic turnover, or the roughly concurrent evolutionary appearance and disappearance of organisms (Crowley & North, 1988; Allmon, 2001). It is also a major factor in determining the geographic range a species occupies (Beaudrot et al., 2019); thus, changes in climate can profoundly influence traits of organisms, species interactions, and the quality of their habitats (Erwin, 2009).

In theory, species may respond to climate change in four general ways: they can evolve adaptations "in place", modify certain intrinsic traits (e.g., behavior, physiology, morphology) within an evolved reaction norm, shift their range to track changes in their habitats, or otherwise go extinct (Pounds et al., 1999; Weeks et al., 2019; Wong & Candolin, 2015). Primates have

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long generation times that preclude rapid accumulation of beneficial genetic adaptations (Angert et al., 2011; Wong & Candolin, 2015), and most modern populations are restricted to fragmented habitats and live at low population densities with limited underlying genetic variation (Struebig et al., 2015). Therefore, the likelihood of an evolved adaptive response in extant populations is unlikely given the rapid pace of modern climate change. Behavioral changes and range shifts are more viable strategies, but observing these processes in long-lived species is difficult. Indeed, there are very few demonstrated links between behavioral variation and climate change, both in animals in general (Buchholz et al., 2019) and primates specifically (Bernard & Marshall, 2020). And, while climate-induced range shifts are relatively well documented among plants (Tomiolo & Ward, 2018) and animals such as insects (Halsch et al., 2021), birds (Møller et al., 2010), and small mammals (Moritz et al., 2008), empirical support remains sparser in the tropics (Beaudrot et al., 2018) and absent for primates (Bernard & Marshall, 2020).

Of the two potentially viable strategies extant primates may employ to respond to climate change on short time scales, some evidence suggests that primates are more likely to modify their behavior than shift their ranges. Primates demonstrate high behavioral plasticity (van Schaik, 2013), and many of their physiological and behavioral qualities (e.g. reproductive seasonality, activity budgets, feeding behavior) are known to vary in response to environmental change (Strier, 2017). Frequent environmental change itself may have driven the evolution of larger brains that, in turn, increases primates' abilities to rapidly adjust their behavior in novel environments (Potts, 1996; Allman et al., 1993; Sol et al., 2008; Sol & Lefebvre, 2000; Wright et al., 2010). In contrast, most primates' ability to shift their ranges may be limited by highly restricted dispersal abilities given geographic barriers, territorial behavior, anthropogenic habitat fragmentation, and the widespread homogeneity of most tropical habitats that would require

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primates to disperse unrealistically rapidly and far to track anticipated changes in their

environments (Arroyo-Rodríguez et al., 2013; Carroll et al., 2015; Kalbitzer & Chapman, 2018;

Loarie et al., 2009; Schloss et al., 2012).

Tropical mountains, however, may present an unusual opportunity for extant primates to

move in response to changing environmental conditions. In homogeneous tropical environments,

mountains emerge as key sources of abiotic and biotic variability (e.g. temperature, precipitation,

and forest structure at Gunung Palung National Park, Indonesia: Marshall, 2009; Marshall et al.,

2014) and primates would not need to travel very long distances to encounter substantially

different habitats (Loarie et al., 2009). Thus, tropical elevational gradients may serve as refugia

during periods of climatic volatility (Malhi et al., 2010). Indeed, shifts and reductions in primate

ranges are increasingly predicted along tropical elevation gradients (e.g. Luo et al., 2015; Stewart

et al., 2020; Struebig et al., 2015; Ahmed et al., 2023). Montane forests may exhibit particularly

high species turnover rates if climate-induced pressures drive lowland species upslope towards

cooler temperatures and "mountaintop extinction" may remove species already adapted to high

elevations (Colwell et al., 2008; Pacifici et al., 2017). Therefore, montane habitats may be

especially dynamic systems during periods of climate change and examining these systems may

provide critical insight into elevational gradients as adaptive landscapes.

The climate on Borneo is getting hotter (+0.083°C yr-1 between 1961 and 2007) and

drier (-0.036mm per year from 1951-2007) with an increase in the intensity of droughts

(McAlpine et al., 2018; Salafsky, 1994). Despite a tangible sense of urgency to understand

heterogeneous species-specific responses to climate change (e.g. Tingley et al., 2012) and thus

recognize which species and populations are most vulnerable, investigations of primates remain

scarce. It also remains unclear how regional climate trends that are most often used in models are meaningful to local biological populations (Maclean & Early, 2023).

This dissertation addresses the effects of climate change on nonhuman primates and investigates the possibility that climate change drives extant primates to shift their ranges in Gunung Palung National Park. Gunung Palung represents one of the few unfragmented (i.e. continuous) tropical elevation gradients where such shifts are possible and data on long-term primate abundance exists. Specifically, I ask three key questions: 1) What is the extent of our knowledge of contemporary climate change and nonhuman primate response, and what important questions must be answered in this field? 2) Have primate ranges shifted along the elevational gradient in Gunung Palung National Park over the last 35 years? 3) What local ecological factors influence these range dynamics, and may climate change be one of the drivers?

1.2 Study site

While Chapter 2 of this dissertation is a global-scale review, the remaining chapters are primarily based on long-term data collected at the Cabang Panti Research Station (CPRS) in Gunung Palung National Park, Indonesian Borneo (1°13'S, 110°7'E). At CPRS, data on primate abundance, weather, and phenology have been collected over 35 years across a 5-1100 m.a.s.l. elevational gradient characterized by two main east-west oriented ridges separated by a river valley (see Fig. 1 in Marshall et al., 2021). CPRS lies close to the coast, resulting in compressed elevational zones and montane forests at relatively low elevations (Cannon et al., 2007; Grubb, 1977; Marshall et al., 2021). These forest types are rich in ecological diversity, with major habitat differences across short spatial distances in geology, soil type, forest structure, floristic behavior, and vertebrate abundances (Cannon et al., 2007, Marshall et al., 2014). The analyses in

this dissertation are the first to investigate primate abundance across the entire CPRS time series. I supplemented this long-term dataset by collecting primate abundance and phenology data in the high-elevation montane forest in 2016 and 2019-2020, where research effort was more limited due to logistical difficulties and general inaccessibility.

I analyze abundance data for the five commonly observed sympatric primate species at CPRS: Western Bornean orangutans (*Pongo pygmaeus wurmbii*), White-bearded gibbons (*Hylobates albibarbis*), Red leaf monkeys (*Presbytis rubicunda*), Long-tailed macaques (*Macaca fascicularis*), and Pig-tailed macaques (*Macaca nemestrina*). Each species ranges across the elevation gradient except for long-tailed macaques, which are specialized to riverine habitats in lowland forests. Primates at CPRS differ in many important traits such as territory size, diet breadth, and degree of habitat specialization, making CPRS ideal to study differential species' responses to environmental change while controlling for ecological differences between sites (Chapman & Chapman, 1999). Further, the elevation gradient at CPRS is unfragmented with no geographic boundaries to inhibit primate dispersal (Schloss et al., 2012). While its containment within a protected area theoretically minimizes the degree to which anthropogenic factors other than climate change may impact resident primates and their habitats, elevated rates of illegal selective logging occurred in the early 2000's (Marshall, 2004), and other anthropogenic stressors are ubiquitous regardless of protected area status (e.g. smoke from large forest fires).

1.3 Chapter Organization

As long-lived, tropical endotherms that live in increasingly fragmented habitats, primates are arguably disproportionately vulnerable to rapid changes in climate. In Chapter 2, I consider why our awareness of contemporary climate change and primates remains so limited and summarize the knowledge and knowledge gaps evident in the small number of published primate

studies that explicitly reference climate change. I find that both empirical and predictive studies are restricted to a narrow pool of species, few of which have documented relationships between primates and climate change over a duration that surpasses a single primate generation. Further, few studies consider concurrent effects of climate change on primates and their habitats, perhaps in part because of the scarcity of long-term data on tropical plant distributions and behavior (Feeley & Silman, 2010).

In Chapter 3, I describe primate distribution patterns over 35 years at CPRS and provide the first empirical evidence for any extant primate population that their ranges are shifting. At CPRS, while most individual primates are behaviorally limited in their dispersal ability, I show that most primates are declining in lowland forests relative to upland forests and the relative abundance of both gibbons and orangutans has increased in upland forests. While these distribution patterns are consistent with general predictions that warming temperatures will push species uphill (Lenoir & Svenning, 2013; Parmesan & Yohe, 2003), I explore additional ecological and anthropogenic processes that may disproportionately decrease lowland primate counts relative to counts in the uplands.

In Chapter 4, I ask specifically whether climate is a potential driver of observed distribution dynamics at CPRS. Commonly, both empirical observations and predictions of range shifts tacitly assume that temperature is a driver of range shifts. While theory suggests that climate is indeed a major driver of distribution dynamics (Parmesan & Yohe, 2003), our understanding of range shifts in extant populations is often based on models that do not consider climate in the context of species' biological environments. I provide evidence that abundance trends along the elevational gradient at CPRS, once food availability is accounted for, are largely not correlated with temperature or precipitation change. I discuss why these relationships may

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not be more widespread, including behavioral restrictions to primate dispersal ability and the fact that local CPRS climate is trending wetter and cooler in contrast with regional Bornean averages.

In the Conclusion, I synthesize the main results of this dissertation and their implications in both conservation and evolutionary contexts. I also discuss several important research directions for future work to pursue.

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Chapter 2[1]: Assessing the State of Knowledge of Contemporary Climate Change and Primates

2.1 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 modern 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.

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[1] Bernard, A. B., & Marshall, A. J. (2020). Assessing the state of knowledge of contemporary climate change and primates. *Evolutionary Anthropology, 29(6)*, 317-331.

2.2 Introduction

Since the advent of the Industrial Revolution, human activities have dramatically changed the global climate (Post, 2013). 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 modern, 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.

2.3 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, 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 1800 A.D., based on the premise that humans began altering the global climate during the Industrial Revolution (Post, 2013).

2.3.1 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 modern 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 (Aarts et al., 2013; Gaston, 2009) as well as the species richness (Willig et al., 2003) and structure (Beaudrot & Marshall, 2019) 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 (Graham & Grimm, 1990). 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 (Thomas et al., 2004) and can inform conservation strategies to mitigate the effects of climate change, such as the location and design of protected areas (Struebig et al., 2015).

2.3.2 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 (Fig. S2.1), and recent global analyses highlight the vulnerability of primates to projected temperature and precipitation changes (Graham et al., 2016) and extreme weather events (Zhang et al., 2019). The availability of information about primates clearly lags behind that of other taxa, however (Fig. 2.1). 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 (Estrada et al., 2017). Recent large-scale assessments of primate conservation specifically acknowledge our limited grasp on the effects of climate change (Estrada et al., 2017; Estrada et al., 2018) or exclude climate change altogether from discussion of threats to primate populations (Li et al., 2018).

2.3.3 Why are primates vulnerable?

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 (Tewksbury et al., 2008), increasing their sensitivity to even small changes in temperature. Second, because most primates are non-migratory (Gnanadesikan et al., 2017) and occupy stable ranges over time, spatial movements

(e.g., long-range dispersal, migration) that mitigate many other species' exposure to changing environmental conditions (e.g., many birds: Samplonius et al., 2018) 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 (Kalbitzer & Chapman, 2018). 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 (Schloss et al., 2012; Carroll et al., 2015). 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 (Graham et al., 2016), 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 (Pacifici et al., 2017).

2.3.4 Climate Change Research on Primates vs. Other Taxa

The first peer-reviewed research article that focused specifically on primates and climate change was published in 1998 (Dunbar, 1998). By that time, the insect climate change literature was sufficiently rich to warrant at least one review article (Woiwod, 1997). 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: Bale et al., 2002) or geographic regions (e.g. Australian marine mammals: Schumann et al., 2013). Within the last decade, there have been multiple books (e.g. Møller et al., 2010) 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 (Korstjens & Hillyer, 2016); reflecting a general paucity of research attention (Fig. 2.1). Additionally, primates are curiously absent from large-scale studies that focus on species most vulnerable to climate change (e.g. Foden et al., 2013) despite their disproportionate vulnerability (Schloss et al., 2012).

Why are primates so underrepresented in climate change research? Here we consider two possibilities. First, it may be a simple mathematical artifact: the Primate clade is less speciose than the other clades depicted in Figure 2.1. 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 (Brooke et al., 2014) predispose primates to attracting disproportionate attention, and indeed, primates are probably the most well-studied tropical taxon (Marshall & Wich, 2016). 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.
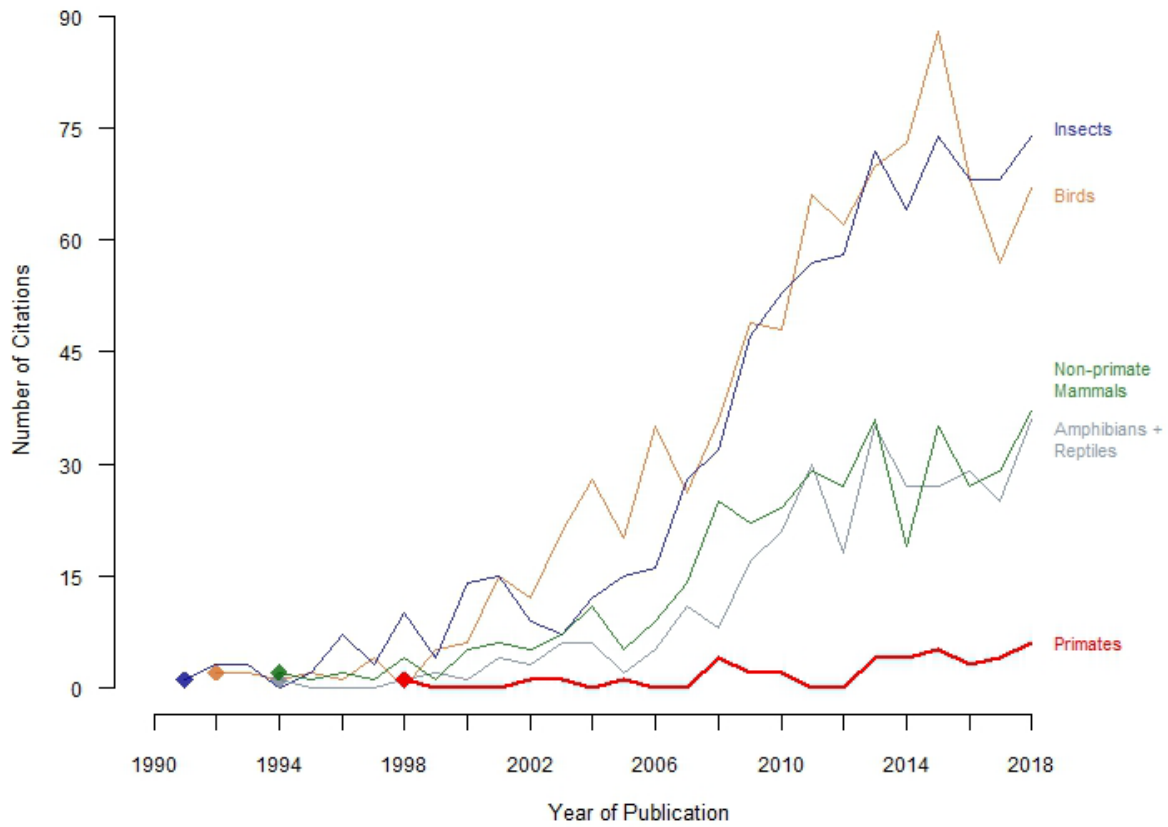
Figure 2.1. Results from a Web of Science literature search (conducted on 27-Feb 2019) tallying climate change studies by broad taxonomic category. Diamonds indicate the first published study. This figure highlights broad differences in research effort among taxa (see Supplementary Text): climate change 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.

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 (Kappeler & Watts, 2012)—much later than research on temperate insects and birds. Perhaps an even more crucial, however, are primates' relatively slow life histories, 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 over time to changes in climate.

2.4 Current Knowledge

2.4.1 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 Supplementary Text 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 Supplementary Text for further

discussion). These excluded studies could certainly further our understanding of the effects of climate change on primates (see Supplementary Text 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 27 June 2017 (n=371 hits) combined with automated email alerts sent to ABB from Web of Science between that date and 07 February 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 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 A1, Appendix I for a full description of the attributes and Table S1 [Bernard & Marshall, 2020, Supplementary Information: Supplemental Information, Table S2.1: https://onlinelibrary.wiley.com/doi/full/10.1002/evan.21874] 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 modern (since 1800 A.D.) 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 addresses 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., 2015) 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 A1, Appendix I). Studies that only referred to climate change in terms of the study's implications (see Supplemental Information for how we determined this) were excluded from our analyses. Using these criteria, we scored 188 papers as "modern" 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 Supplemental Text 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) that should not be attributed to climate change. To assess whether restricting our

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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 Supplemental Information (Figs. S2.2, S2.3, S2.4, S2.5) 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: 1) assess the distribution of current scholarship as a function of phylogeny and geography; 2) consider the relative amount of information available about climate-related changes in primates, their habitats, and their foods; 3) assess the temporal scope of published observational studies of the effects of climate change on primates; and 4) briefly review current predictions and observed patterns relevant to primate responses to climate change.

2.4.2 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 were 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 under-studied.

Fifty of the 79 extant primate genera (taxonomy following Estrada et al., 2017) are represented in our primate climate database (Figs. 2.2, 2.3). Of these 50 genera, only 18 have more citations than
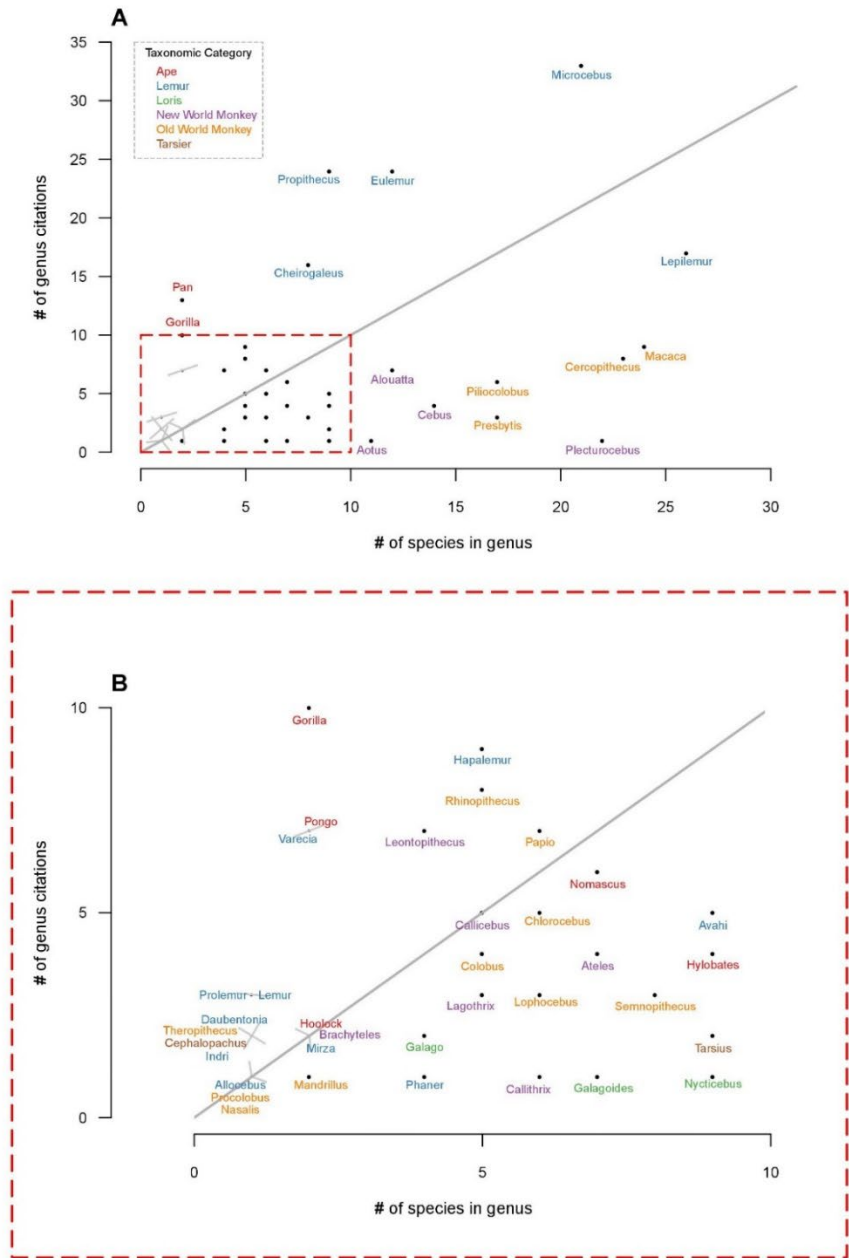
Figure 2.2. Phylogenetic distribution of climate studies (combining quantitative and qualitative research; see SI) addressing **A)** all genera and **B)** genera within the 10x10 grid (for visual clarity). The dotted line denotes a 1:1 correlation between the number of species in a genus and the number of climate studies addressing that genus; species under the line are underrepresented given their diversity, and species over the line are overrepresented.

would be predicted if every species in the genus was the focus of one climate change study (Fig. 2.2). 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 Old World Monkeys (OWM), seven (28%) are New World Monkeys (NWM), three (12%) are lorises, three (12%) are lemurs, two (8%) are apes, and one (4%) is a tarsier. These results support prior indications (Marshall et al., 2016) 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 (Fig. 2.2), 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 NWM species, 29 of 172 OWM species, and 2 of 11 tarsier species (Fig. 2.3A).

Of the six taxonomic groups, OWM and NWM are the most species-rich, and inequitable effort across these groups with respect to phylogeny is particularly noticeable. Based on their residual values (Fig. 2.2), the five least-represented genera include four OWM (*Macaca*, *Cercopithecus*, *Presbytis,* and *Piliocolobus*) and one NWM (*Plecturocebus*). Of the 144 unrepresented NWM species, 80 have no represented congener. Similarly, of the 143

unrepresented OWM species, 50 have no represented congener. Several of these unrepresented genera are particularly species-rich themselves, including *Trachypithecus* (OWM, 20 species), *Pithecia* (NWM, 16 species), *Mico* (NWM, 13 species), and *Saguinus* (NWM, 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 (Fig. 2.4A). 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 (Fig. 2.4B). 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 (Marshall et al., 2016; Bezanson & McNamara, 2019). This bias likely has several underlying reasons, including apes' large body sizes, charisma, or phylogenetic proximity to humans(Marshall & Wich, 2016). The bias in favor of work on lemurs is not, however, consistent with broader publication patterns in the primatology literature (Bezanson & McNamara, 2019), 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: Sussman et al., 2012). In addition, lemurs have shorter lifespans, increasing the probability that researchers can observe effects of climate change on lemur
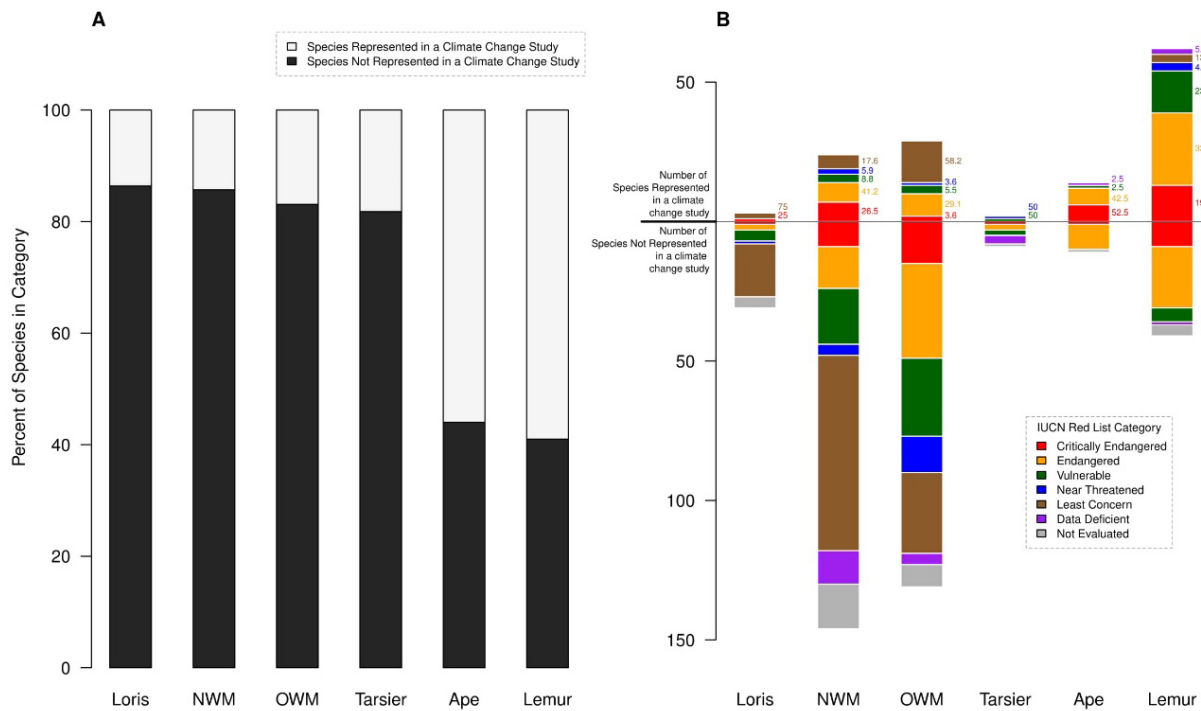
Figure 2.3. Taxonomic diversity of primates in climate studies. **A)** Percent of species represented and unrepresented in our database. Bars are ordered left to right by increasing percentage of species represented. **B)** Bar height indicates counts of represented (above horizontal line) and unrepresented (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.

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A
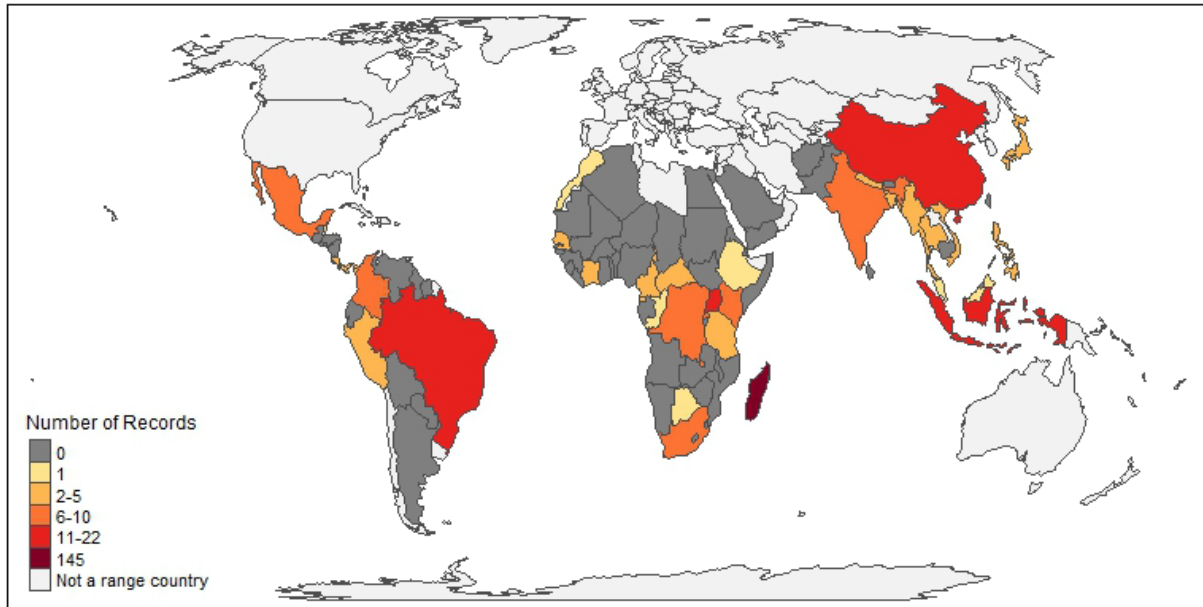
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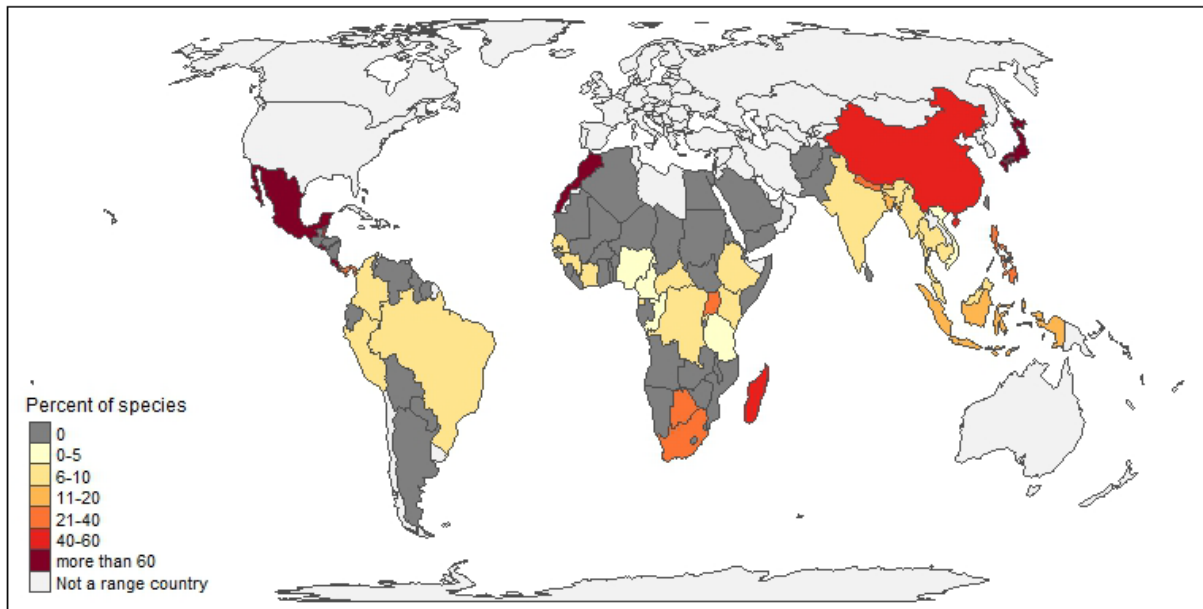
Figure 2.4. A) Number of focal primate records and **B)** percentage of resident species in climate studies, by country.

populations. Among primates, heterothermy (whereby primates modulate their metabolic rate to decrease their energy expenditure) is most common within the Cheirogaleidae family (Dausmann, 2014), and climate studies may target these species given the high probability that climate directly influences their physiological function.

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 (Estrada et al., 2017). Among primates, lemur populations are disproportionately exposed to seasonal powerful cyclones (Zhang et al., 2019) that may be intensifying due to climate change (Elsner et al., 2008), 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 (Pacifici et al., 2017), 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 (Graham & Grimm, 1990; Pacifici et al., 2017; Tingley et al., 2009). 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 (Pounds et al., 2006).

Because ecological traits are not evenly distributed across the primate phylogeny, taxonomic gaps in knowledge may produce holes in our ecological knowledge as well. We analyzed the residual values from the distribution of genera in Figure 2.2, and did not find systematic biases among genera with respect to body size, percent frugivory, or group size (Fig. S2.6). However, holes in our ecological knowledge still exist. With 82% 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 OWM species (Estrada et al., 2017), only 13 (or 14%) are represented in the database (Fig. 2.3B). Lorises (1 of 7: 14%), NWM (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 (Graham et al., 2016) 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*

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geoffroyi, *Cercocebus galeritus*, and *Macaca sylvanus*) are the subject of just three climate

change studies combined (Korstjens et al., 2010; Gonzalez-Zamora et al., 2011; Ramos-

Fernández et al., 2013).

2.4.3 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. 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 1) primates themselves (e.g. physiological tolerance, social behavior, demography),

2) primate habitats (e.g. habitat suitability, forest connectivity), and 3) primate foods (e.g.

quality, phenology, availability). While food is an important part of the resource base that defines

a habitat (Vrba, 1992), 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 (Marshall, 2010). Further, we do not

incorporate food availability 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., 2015).

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

(Parmesan, 2006), and it is important to assess how climate change may differentially affect

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these elements (Voight et al., 2003). 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 (Vrba, 1992). 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 (Graham & Grimm, 1990), as well as interpret the different timescales on which species respond. For example, while plants are more likely to migrate than adapt in place (Huntley, 1991), primates may more readily change their behavior in place given their dispersal restrictions (Schloss et al., 2012) 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, 2007) 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 Supplementary Text). 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 (Olupot, 2009) 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 (2013) found that changes 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. (2012) 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 (2011) compared how both primate density and forest structure responded to a cyclone, and multiple studies (Ramos-Fernández et al., 2013; Herrera et al., 2018) have generated distinct species distribution models for primates and their important food trees. Raghunathan and colleagues (2015) also investigated changes in food and habitat by modeling the future distribution of important food and sleeping tree species for two *Leontopithecus* species.

2.4.4 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 (Fig. 2.5). The 27 records of food analyses range from less than one 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 (2012), 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) comparisons may suggest changes over time, but generally do not permit robust extrapolation of the results into temporal trends.

2.4.5 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
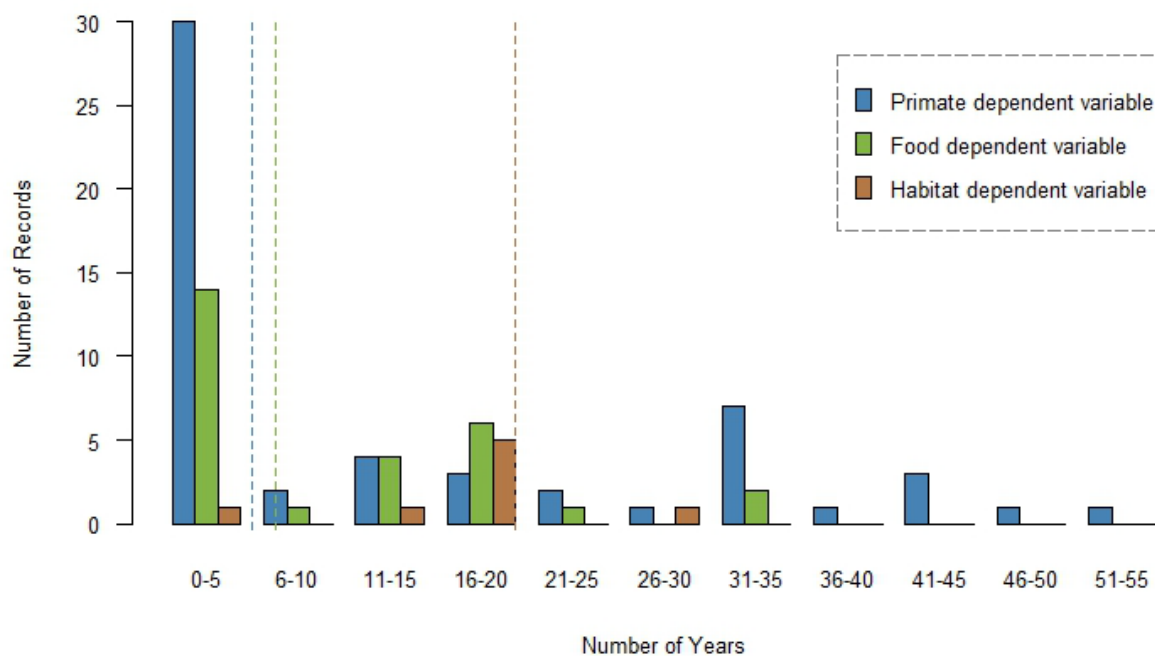
Figure 2.5. Frequency distribution of time series data used in quantitative climate studies. Vertical dotted lines indicate the median number of years for each variable type (e.g., the blue line shows the median duration of time series datasets using primate dependent variables). These data are from 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.

have done this (Korstjens & Hillyer, 2016; Kalbitzer & Chapman, 2018), Rather, we highlight patterns that have emerged from studies that draw explicit links between modern 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 (2015) 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*]: Clee et al., 2015). Similarly, predictions of changes in habitat suitability can differ dramatically among protected areas currently inhabited by large primate populations (Meyer et al., 2014).

No study in our database reported a modern range shift in primates in response to climate change. Grueter and colleagues (2013) did observe that food species frequently consumed by mountain gorillas (*Gorilla beringei beringei*) had shifted up- or down-slope 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 (2015) 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 meters. More distant projections for 2070-2080 often predict more

severe population reductions surpassing 80% (e.g. snub-nose monkeys: Luo et al., 2015; lion tamarins [*Leontopithecus* spp.]: Meyer et al., 2014) and even complete extirpation (Hoolock gibbons [*Hoolock hoolock*]: Alamgir et al., 2015).

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: Campos et al., 2017; offspring sex ratio: Kühl et al., 2012). Such changes (e.g. rising temperatures, more severe droughts) are often deleterious for primates, resulting in lower birth rates (northern muriquis [*Brachyteles hypoxanthus*]: Wiederholt & Post, 2011), declines in reproductive output (white-faced capuchins [*Cebus capucinus*]: Campos et al., 2015), or increased offspring mortality (ibid.). These results indicate that climate change will likely threaten many populations' persistence (Wiederholt & Post, 2011).

Empirical results indicate that increasingly dry conditions may be particularly problematic for primates. Food production tends to be lower in the dry season (Chapman et al., 2006; Pichon & Simmen, 2015) and lower quality food has demonstrable negative effects, including reductions in individual health and lower population densities (gray-brown mouse lemurs [*Microcebus griseorufus*]: Eva-Maria et al., 2011). More severe droughts and longer dry seasons also lead to decreased reproduction (northern muriquis and brown woolly monkeys [*Lagothrix lagotricha*]: Wiederholt & Post, 2011). 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 (Eronen et al., 2017).

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: Campos et al., 2017). These evolved strategies may allow primates to persist under unpredictable environmental conditions(Johnson et al., 2011) and during periods of negative energy balance(Wessling et al., 2018). 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 (Fahrig, 2003).

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(Campos et al., 2017). 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% (Gursky et al., 2017), Gray-headed lemur (*Eulemur cinereiceps*) abundance was similar before and after a cyclone (Johnson et al., 2011). This inconsistency is unsurprising, given that climate changes themselves will differ among regions (Graham et al., 2016), 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,(Marshall et al., 2016) 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 (Kappeler & Watts, 2012) and

researchers can therefore apply robust 50+ year longitudinal datasets to investigate changes through time in an increasing number of primate species.

2.5 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 (Walther et al., 2002): 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 (Johnson & Sherry, 2001). Emerging methods are beginning to incorporate such factors (e.g. to predict range shifts: Lenoir & Svenning, 2015) 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.

2.5.1 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%) within species distribution models employ Maximum Entropy software (Fig. S2.7). 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, (Araújo & Peterson, 2012; Thorne et al., 2013) can be strongly impacted by sampling bias (Kramer-Schadt et al., 2013), and often conflate fundamental and realized niches by failing to incorporate biotic interactions into species' ranges (Pacala & Hurtt, 1993). To the greatest extent possible, it is imperative that these models incorporate biogeographical and ecological attributes of species (Araújo & Peterson, 2012) in conjunction with broadened efforts to investigate observed habitat changes that may be attributable to climate.

2.5.2 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 (Grueter et al., 2013; Raghunathan et al., 2015) through observations of fruiting tree behavior(Chapman et al., 2006). 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 (Marshall & Wrangham, 2007). 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(Marshall & Wrangham, 2007). Recent studies that examine changes in nutrient

composition of primate foods and leaf quality over time (Pichon & Simmen, 2015; Rothman et al., 2015) provide valuable models for how knowledge may be advanced in this area.

2.5.3 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., 2015; Ramos-Fernández et al., 2013). 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 (Thorne et al., 2013). 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: Lenoir & Svenning, 2015). It could also be that models fail to accurately predict changes because future climates may have no modern analogues (Prentice et al., 1992).

2.5.4 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 (Pacifici et al., 2017). For example, even when multiple primate species share the same habitat, species respond to environmental change differently (Herrera et al., 2018). Recent research suggests that traits vary substantially across species ranges (MacLean & Beissinger, 2017), and species' responses may vary in part due to the strong influence of local weather conditions (Campos et al., 2017). This suggests that species traits exist in a complex interplay with "region-specific" factors (Tingley et al., 2009), 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 (Arcadi, 2018) 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 proposed that climate responses may be organized into "functional groups," such that differences within the groups are smaller than those between groups (Lawton, 1995). If it could be done in a robust manner, achieving this functional standardization—whether by taxonomy, geography, habitat, dietary regime, behavior, etc.—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 (Kamilar, 2009).

2.5.5 What role will behavioral plasticity play?

The ability of primates to disperse to track changes in their habitat is limited (Schloss et al., 2012; Carroll et al., 2015), 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 (Buchholz et al., 2019). 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 (Lehmann et al., 2010), and the scope of primates' flexibility itself may be progressively constrained by increases in temperature (vervet monkeys [*Chlorocebus pygerythrus*]: McFarland et al., 2014). 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 (Kalbitzer & Chapman, 2018).

2.5.6 How does climate change interact with other threats?

Climate change will likely exacerbate the negative consequences of other human-induced threats. For example, habitat fragmentation restricts genetic diversity and may therefore limit primates' ability to evolve in response to rapid environmental change (Gregory et al., 2014). Climate change is also likely to influence rates of disease transmission and pathogen outbreaks fueled by warmer temperatures may accelerate population declines much more rapidly than otherwise anticipated (Pounds et al., 2006). 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 (Brodie, 2016). 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 (Brodie, 2016). 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 (Mantyka-Pringle et al., 2012).

2.5.7 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 (Dausmann, 2014; Ross, 1992), 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 (Lovegrove et al., 2014). Multiple primate species modulate their metabolism and energetic expenditure based on external temperatures (Dausmann, 2014), 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 (Welbergen et al., 2008). 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°Celsius (Stitt & Hardy, 1971). 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: Wessling et al., 2018), as well as analyses that strive to incorporate primate physiology into mechanistic climate change models (Lovegrove et al., 2014).

2.5.8 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 (Menéndez et al., 2006) and broadly between animals and plants (Davis, 1986), 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 (Selwood et al., 2015), 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" (Dullinger et al., 2012) 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.

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2.7 Supplemental Information

2.7.1 Supplemental Figures
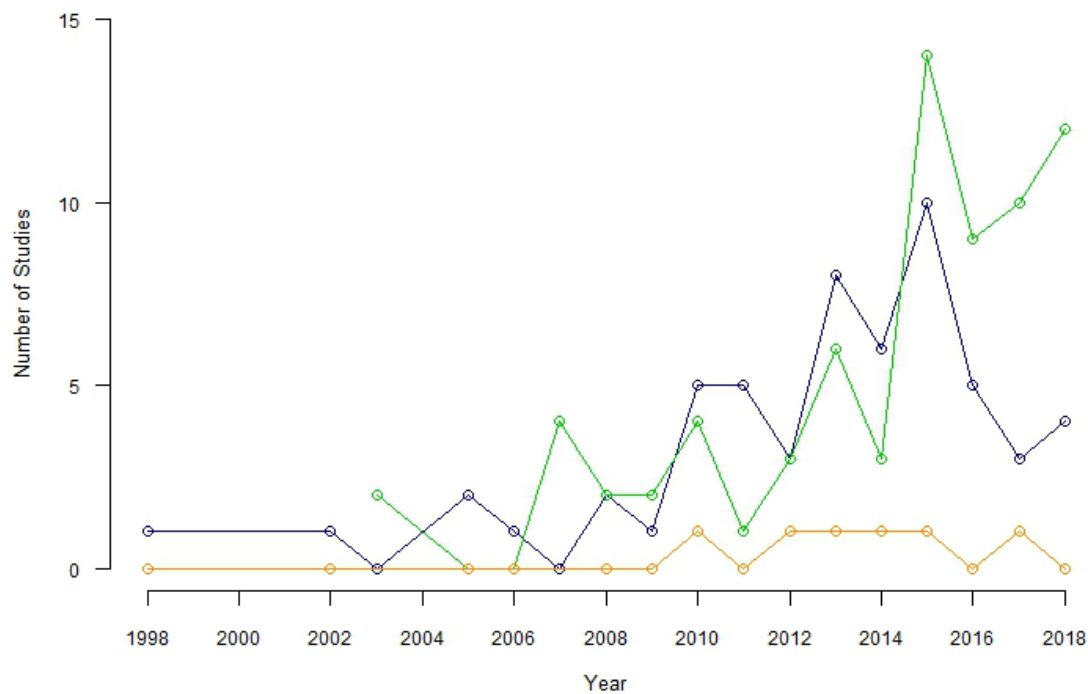
Figure S2.1 Temporal variation in the number of primate studies related to climate change returned by our literature search. The blue line indicates papers that used the words "climate change" or "global warming" in their title or keywords. The yellow line depicts papers that include the words "climate change" or "global warming" in their title or keywords but were not primarily focused on climate change (i.e., a subset of the papers indicated by the blue line). The green line depicts papers that used the words "climate change" or "global warming" sparingly in the text (although not in the title or keywords) but were not focused on climate change. For a full description of these distinctions, see Table A1, Appendix I.
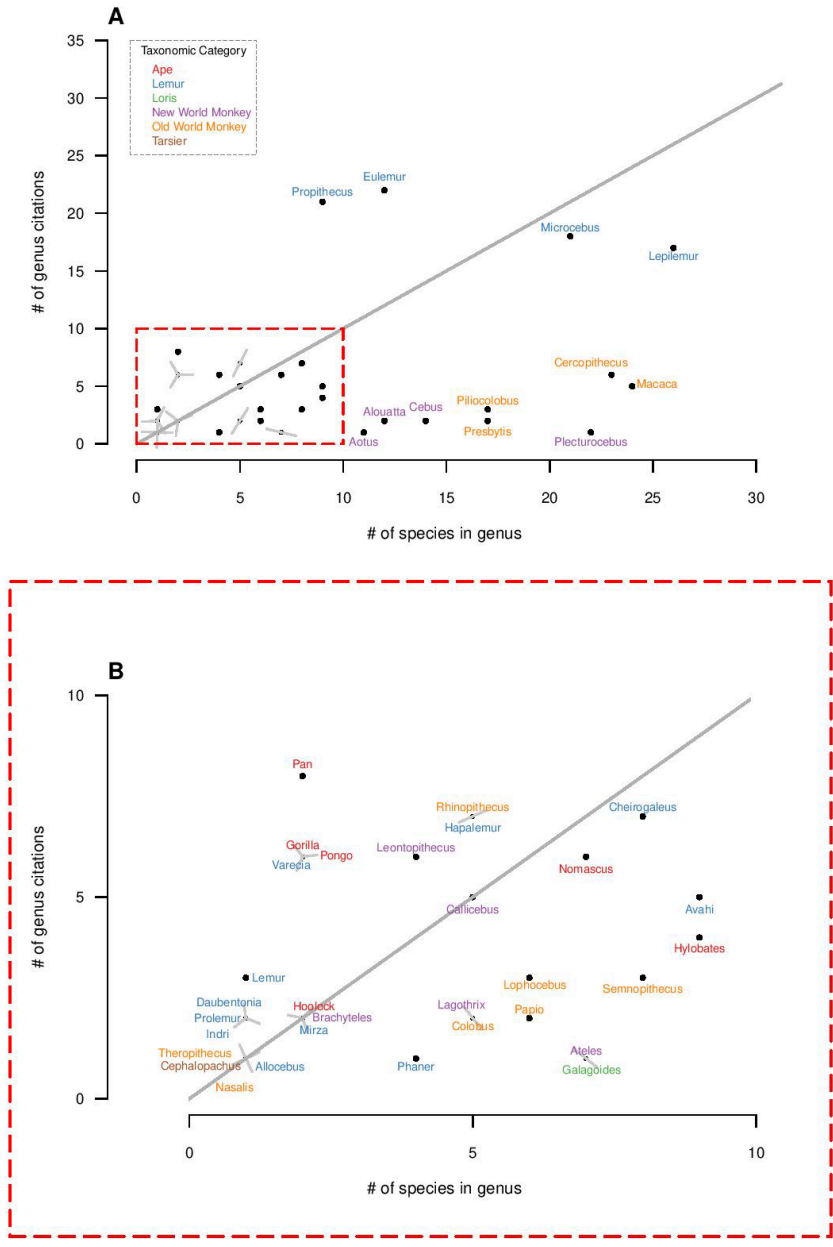
Figure S2.2. Phylogenetic distribution of climate studies, as in Figure 2.2 from main text, including only the subset of studies in our database that span at least 1 year in duration.
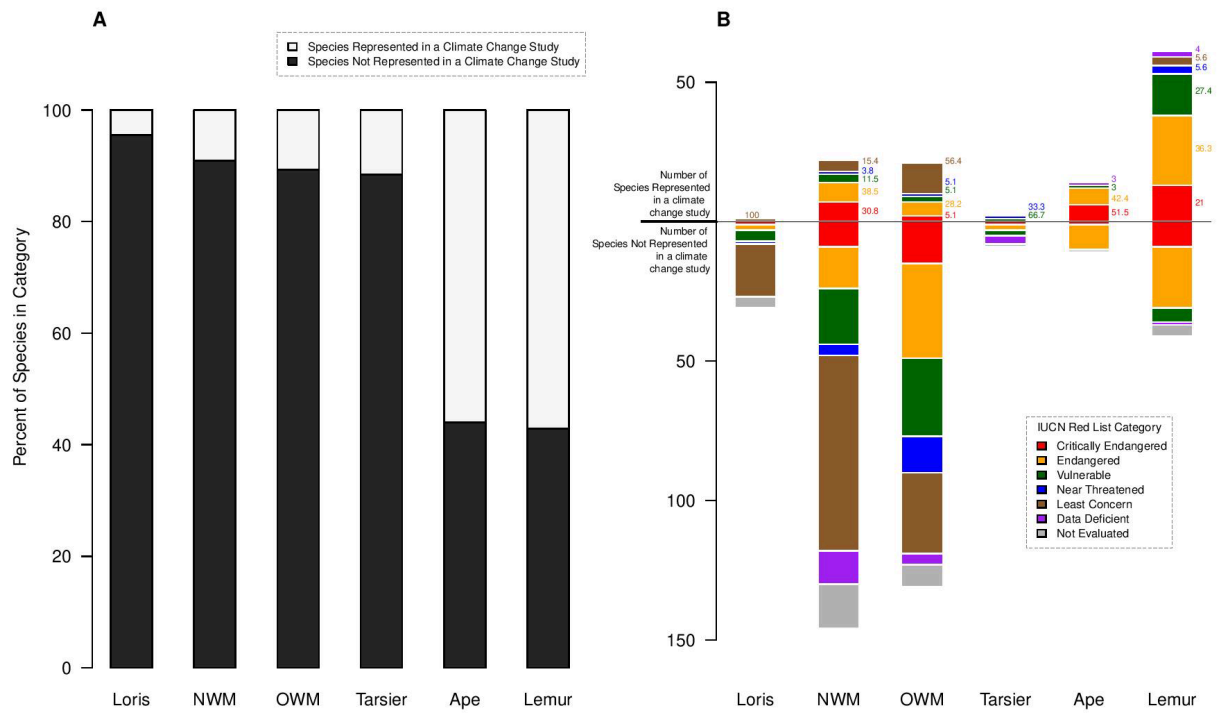
Figure S2.3. Taxonomic diversity of primates in climate studies, as in Figure 2.3 from main text, including only the subset of studies in our database that span at least 1 year in duration.

A
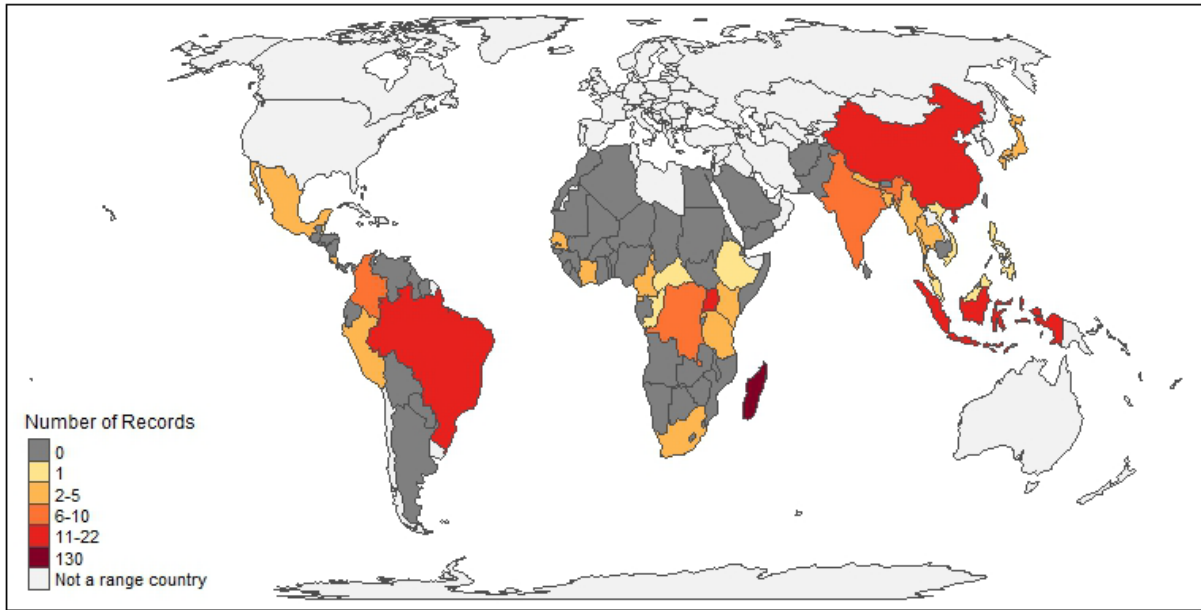
B
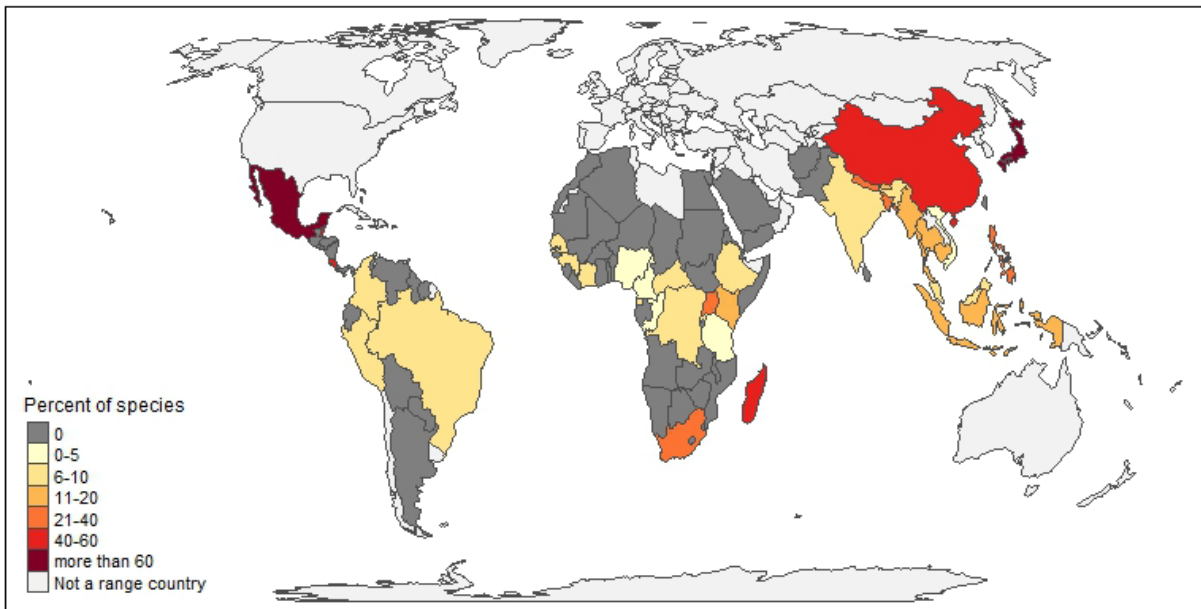
Figure S2.4. Focal primate records by country, as in Figure 2.4 from main text, including only the subset of studies in our database that span at least 1 year in duration.
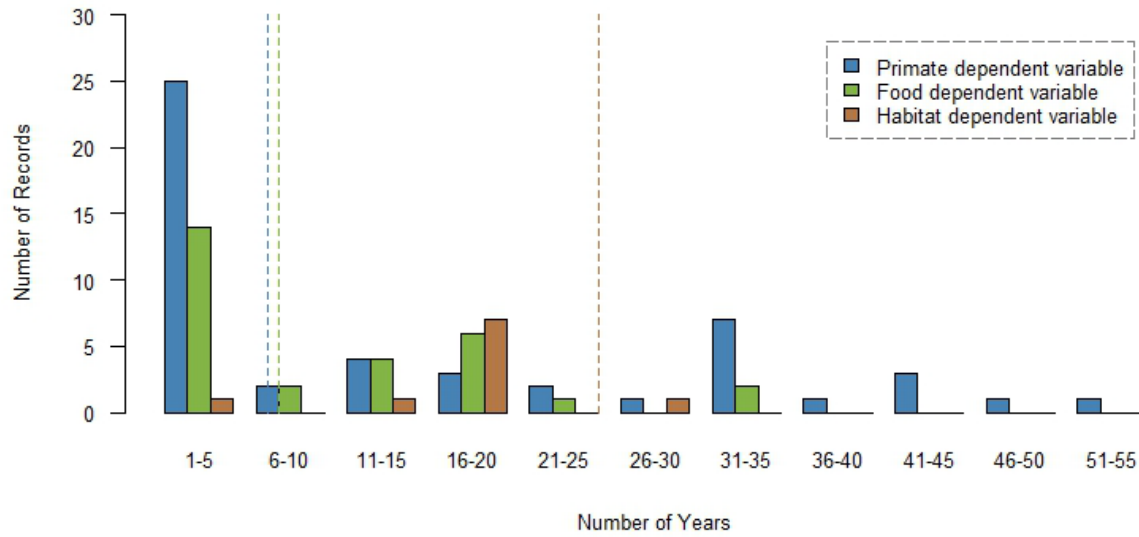
Figure S2.5. Frequency distribution of time series data used in quantitative climate studies, as in Figure 2.5 from main text, including only the subset of studies in our database that span at least 1 year in duration.
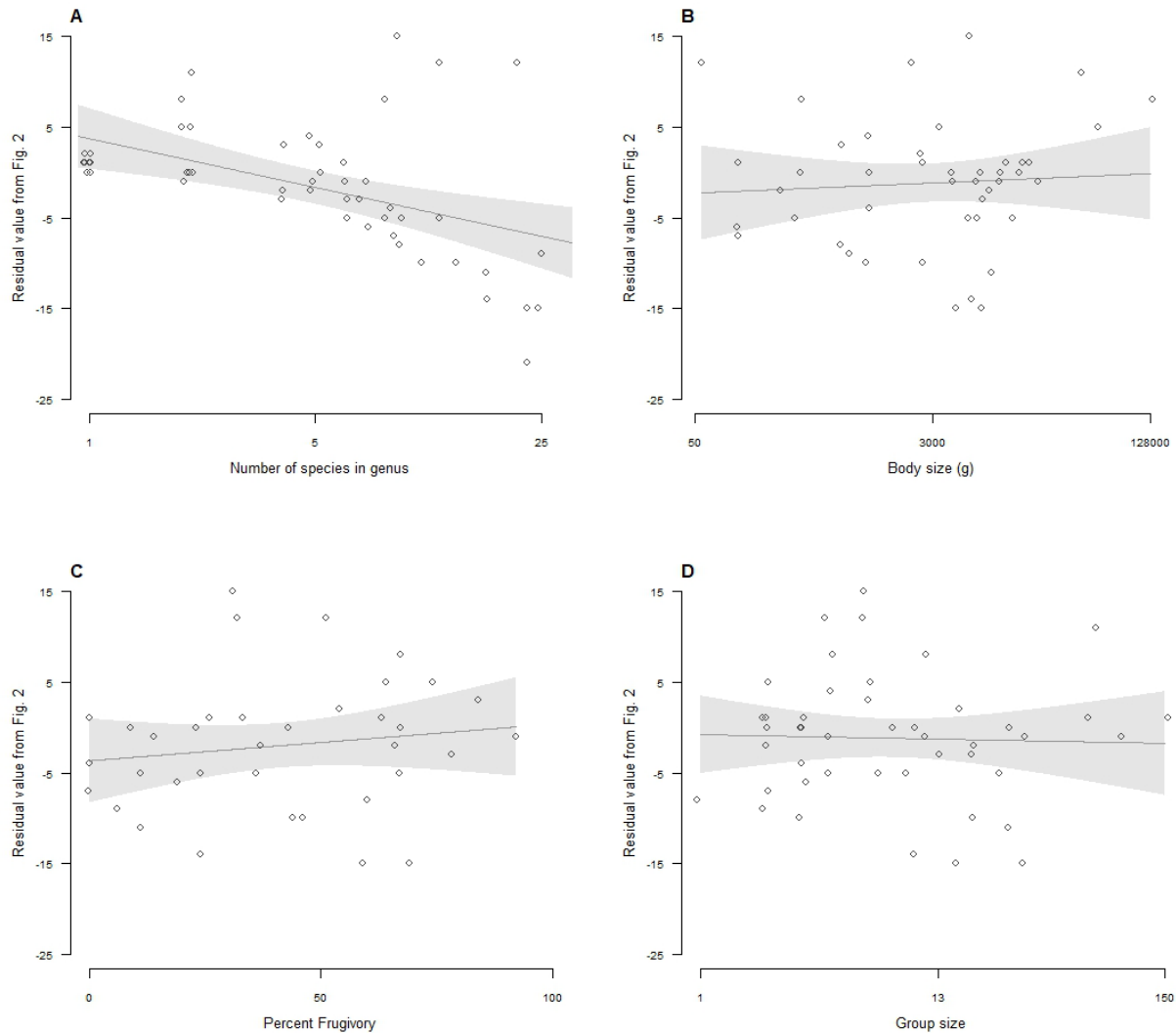
Figure S2.6. Linear models associating relative representation in the climate change literature (Fig. 2.2 residual values) with primate and environmental variables. Values on x-axis were jittered (i.e., a small random number was added to each point) for visual clarity of the points. All predictor variables were log-transformed except for Percent Frugivory. Shading represents 95% confidence intervals. **A:** Number of species in the genus (β = -3.34, r^2 = 0.22, p < 0.0005) **B:** Body size (β = 9.514*10^{-5}, r^2 = 0.08, p = 0.06) **C:** Percent frugivory (β = 0.04, r^2 = 0.03, p = 0.39) **D:** Group size (β = 0.01, r^2 < 0.01, p = 0.79) Data on body size, percent frugivory, and group size come from Decasien et al. (2017) Each point represents a genus. Only the number of species in the genus was a strong predictor of relative representation in the climate change database.
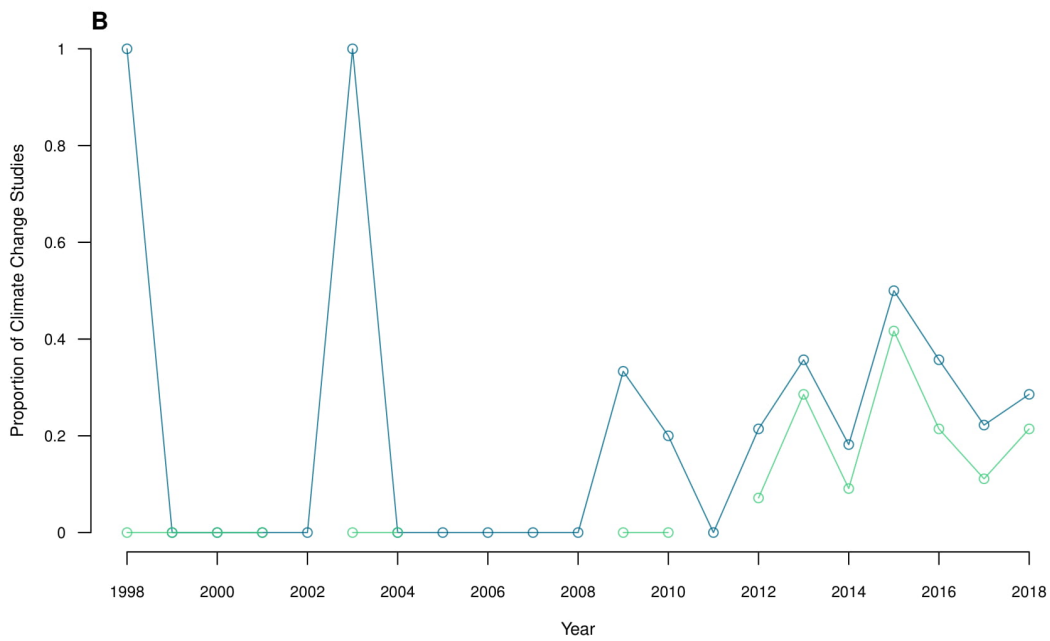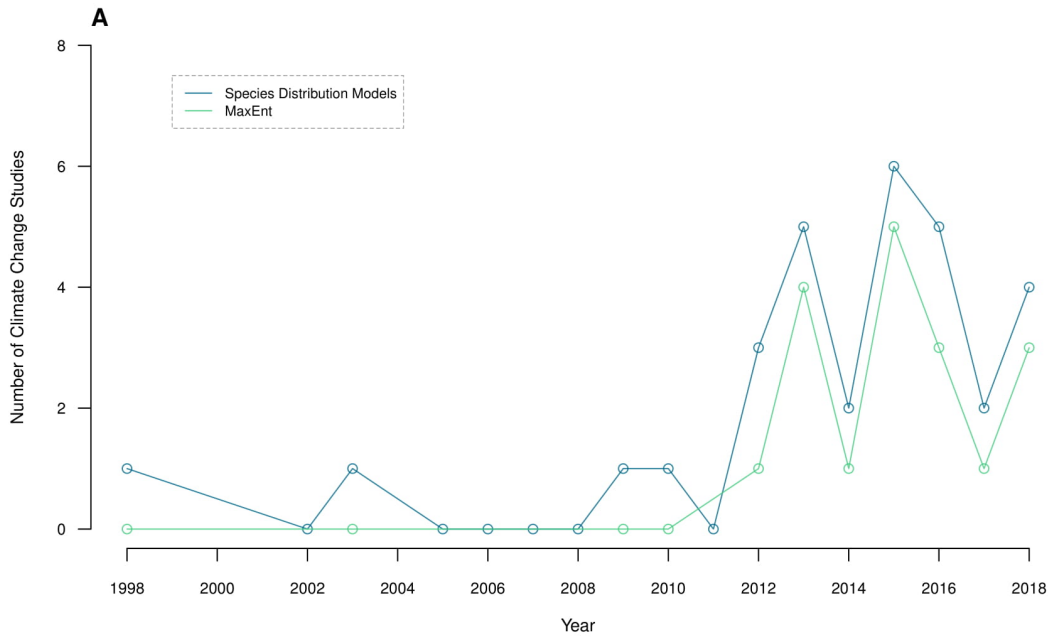
Figure S2.7. The **A)** number of and **B)** proportion of studies in our database that include species distribution models and Maximum Entropy software within primate climate change studies.

A

B
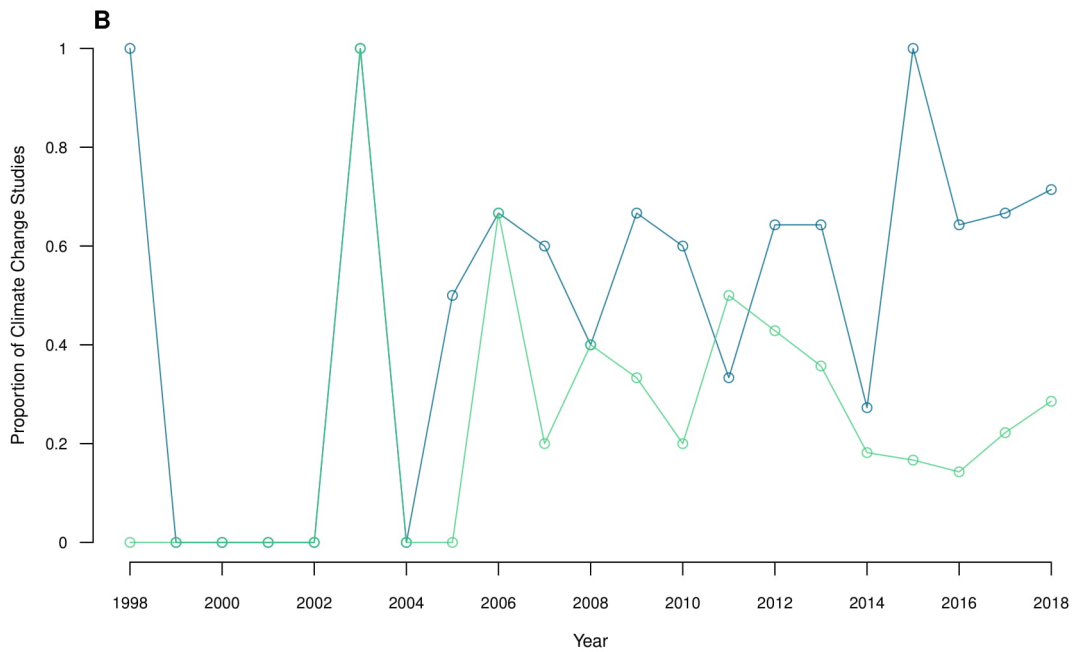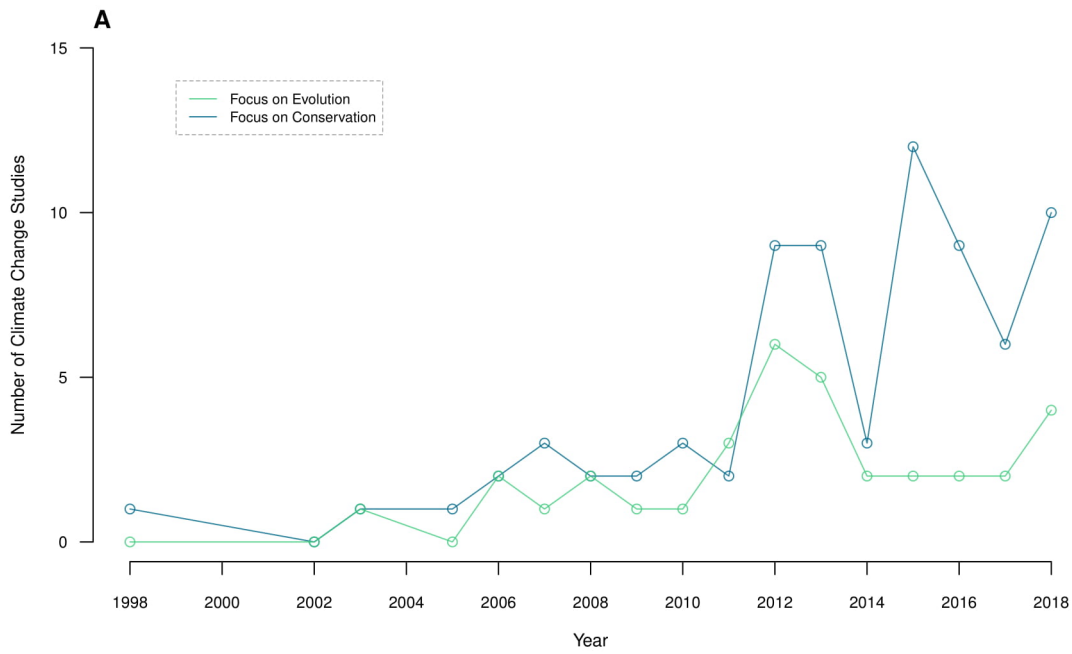
 Figure S2.8. The **A)** number of and **B)** proportion of studies that focus on the subjects of conservation or evolution within the primate climate change literature. See Table A1, Appendix I for a complete description of keyword identification and our determination of a subject "focus."

2.7.2 Supplementary Text

2.7.2.1 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). (Post, 2013; Gilman et al., 2010)

Extinction debt - "In single species, the number of proportion of populations expected to eventually become extinct after habitat change" (Kuussaari et al., 2009). As it applies to climate change, the range a population occupies may no longer climatically suitable, resulting in deterministic population declines (Dullinger et al., 2012).

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 (Dausmann, 2014).

Intraspecific behavioral flexibility – variability in behavior within a species at the individual, group, or population level that may or may not have adaptive value (Strier, 2017).

Longitudinal data – data collected on a focal variable (e.g. individuals, groups, populations, climate metrics) systematically over time useful for measuring change.

Long-term phenological data – longitudinal phenology datasets, e.g. 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 (Chapman et al., 2005; Cannon et al., 2007).

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 (Phillips et al., 2006 ; Kramer-Schadt et al., 2013).

Range shift - species or populations shift their geographic range in response to a change in the environment, land use, or management regimes (Tomiolo & Ward, 2018). Climate-induced shifts habitually occur across latitude or elevation gradients (Chen et al., 2011).

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 (Brodie et al., 2011).

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).

2.7.2.2 Figure 2.1 search terms

We searched the scientific literature on 27 February 2019 using Web of Science to compare climate change research effort by taxon using the following search terms (Fig. 2.1). "TS" indicates a "topic search," and "TI" indicates a "title search."

Primates:

TS = (primate* OR monkey* OR lemur*) AND TI=("climate change" OR "global warming")

Amphibians and reptiles:

TS=(frog* OR amphibian* OR snake* OR reptile*) AND TI=("climate change" OR "global warming")

Insects:

TS=(insect* OR butterfl*) AND TI=("climate change" OR "global warming")

Non-primate mammals:

TS=(mammal* NOT (primate* OR monkey* OR *lemur*)) AND TI=("climate change" OR "global warming")

Birds:

TS=(bird*) AND TI=("climate change" OR "global warming")

This search was not meant to be comprehensive, as we restricted the taxonomic keywords to very general terms and required use of "climate change" or "global warming" in the title. Nevertheless, we have no reason to expect that this sampling method biased in favor of or against certain taxonomic groups and thus contend that it accurately reveals broad differences among taxonomic groups.

2.7.2.3 Keywords for Climate Database

We used the following search terms to generate the climate change research database. "TS" indicates a "topic search."

TS = (monkey* OR loris* OR bushbab* OR galago* OR potto* OR lemur* OR sifaka* OR aye-aye* OR tarsier* OR howler* OR marmoset* OR tamarin* OR capuchin* OR saki* OR baboon* OR macaque* OR mangabey* OR mandrillus OR vervet* OR kipunji* OR colobus* OR guenon* OR langur* OR surili* OR lutung* OR gibbon* OR siamang* OR gorilla* OR bonobo* OR orangutan* OR chimpanzee*)

AND

TS = ("global warming" OR "climate change")

2.7.2.4 Limitations of search terms

Many primate papers mention specific primate genera or species but never use the word "primate." Therefore, we developed search terms that included specific primate clades. As a result, we recognize that our search results may exclude valuable research that focuses on 1) habitats lived in by primates, but does not mention the primates themselves, 2) important primate food sources, but does not also mention specific primates that feed on them, and 3) studies with a much wider taxonomic breadth that do not mention specific primates, but rather isolate "primates" as a distinct mammalian order (e.g. Pacifici et al., 2015; Pacifici et al., 2017). Our search terms also included specific primates, but no food-specific nomenclature.

We do not believe the exclusion of these studies biased our results and are confident that the vast majority of relevant studies are included. However, we also recognize that by their nature, systematic literature searches do not uncover every relevant study. Below we briefly note examples of studies that provide valuable information about primates and climate change but were not captured by our search terms.

Two studies from Kibale National Park (Chapman et al., 1999; Chapman et al., 2005) that

focus on changes in fruiting and flower phenology through time were not caught by our

keywords—including one that directly addresses the importance of climate change—because

neither study mentions a primate. For similar reasons, our search terms did not capture two long-

term habitat studies from Barro Colorado Island (Condit, 1998; Condit et al., 1996). Neither did

our search capture studies in which the terms "climate change" or "global warming" did not

appear, even if the study investigated correlations between climate and primates (e.g. Marshall et

al., 2014; Mitchell et al., 2009).

2.7.2.5 The Influence of Time on Species Response to Climate Change

As noted in the main text, we did not impose a minimum duration cutoff to consider a

study a "climate change study." While it is true that climate change itself may typically occur

over periods of "decades or longer" (IPCC, 2013), p. 126), any cutoff we might impose would be

arbitrary. We cannot generalize the amount of elapsed time necessary for long-term climate

changes to impact biological systems, and therefore cannot discount the potential of short-term

studies to inform how species may be impacted by climate change. Below, we expand on this

perspective through four primary arguments.

First, it is increasingly recognized that evolutionary change can occur quite rapidly.

Evolutionary biologists increasingly question conventional wisdom that suggests the pace of

evolutionary time is slower than ecological time (Slobodkin, 1961), and recent work in the

Galapagos (Lamichhaney et al., 2017) adds to the growing body of literature that describes

observations of rapid evolutionary change and questions traditional assumptions about how

quickly evolutionary change can occur (Hoffmann & Sgrò, 2011).

Second, to impose a minimum duration cutoff would obscure meaningful variation in the scope and breadth of potential biotic responses to climate change. Not only are these responses partially conditioned by species-specific effects, but the time necessary to demonstrate that a change has occurred may vary among the types of response. Climate-induced range shifts in insects may occur "rapidly" if observed over 25-30 years (Chen et al., 2011; Lehikoinen et al., 2013) but multiple climate-induced amphibian population crashes occurred in less than one year (Pounds et al., 1999). On an even shorter timescale, primate behavior and physiology habitually changes from one hour to the next (Lubbe et al., 2014; Strier, 2017). While some variation (e.g. daily fission-fusion dynamics) is clearly not a direct result of climate change, individual behavioral adjustments are firmly within the purview of phenological responses to climate change (Charmantier et al., 2008). Life history parameters may also affect the amount of time over which species respond to climate change. Because the range of primate lifespans in the wild is so broad (e.g. 4 years for mouse lemurs: Zohdy et al., 2014; 55+ years for chimpanzees: Austad & Fischer, 1992) the time required for researchers to assess population stability (Connell & Sousa, 1983) varies considerably.

Third, establishing that a change has occurred requires a departure from a baseline condition (i.e. a change, relative to what?). These baseline conditions can potentially vary with respect to the species being studied (e.g. variation in life history), the time over which they are studied, and where they are studied. Natural climate forcings occur on vastly wide-ranging timescales, ranging from 100,000-year Milankovitch cycles to decadal-scale El Niño–Southern Oscillation cycles. While a "rapid" climate change in recent evolutionary history may occur over a 1000-year period (the Younger-Dryas: Hannah, 2011), "rapid" human-driven climate change may occur on an annual timescale (Post, 2013). Additionally, shifts in climate can be measured

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through multiple modes, including shifts in averages, seasonality, or extremes, and each mode may require a different amount of time to demonstrate that a change has occurred. With respect to where primates are studied, vulnerability to climate change is highly contingent on population size (e.g. Pounds et al., 2006), and small populations are more likely to exhibit rapid measurable responses to climate change than large populations. Primates also live in a wide range of seasonal and non-seasonal habitats (Brockman & van Schaik, 2009). Because there is inherently more natural variability in seasonal habitats relative to less-seasonal habitats, longer time series datasets may be required to measure species responses in seasonal habitats.

Finally, the effect of time does not necessarily operate as a linear function, as may be the case if species' responses to climate change were both consistent and continuous through time. Neither condition, however, is necessarily true. Climate can interact with other factors to increase the rate at which small climate changes have large effects (e.g. species viability as impacted by the spread of disease (Pounds et al., 2006), thereby distorting any timescale suggested by a model that solely relates species with climate. Changes "over time" can also be demonstrated with only two data points (before and after) rather than continuous data in the case of extreme weather events. Because the severity of extreme weather events is likely impacted by human-induced climate change (Coumou & Rahmstorf, 2012), variation in a primate trait before and after such an event (e.g. a hurricane: Pavelka et al., 2003) could also be attributed in part to climate change. Additionally, extreme temperatures can be detrimental for certain species if a physiological threshold is crossed: in 2002, over 3500 flying foxes died within a day in Australia during a 42°C extreme temperature event (Welbergen et al., 2008).

2.7.2.6 Additional notes on large-scale studies excluded from our analyses

As noted in Table A1 (Appendix I) we labeled certain studies with a "Basal taxonomic level" designation (n=7). These studies are large in scale and incorporate many primate species. While most of these studies met our criteria either for a qualitative or quantitative climate study, we excluded all of them from our phylogenetic analyses and most from our geographic analyses. We excluded two studies (Estrada et al., 2017; Trayford & Farmer, 2013) from each analysis because they did not quantitatively relate primates to changes in climate. We excluded Korstjens et al. (2010) from the geographic analyses because of the difficulty we faced in assigning spatial locations to the study's focal primates. We included Nadler & Roos (2017) and Li et al. (2018) in our geographic analysis, only because the studies restricted their scope to primates within Vietnam and China, respectively. We also excluded Graham et al. (2016) from both phylogenetic and geographic analyses. This study meets our criteria for a quantitative climate change study by assessing the future exposure of 419 primate species to changes in temperature and precipitation. Because the study would add one single data point for most extant primate species (including those that are otherwise unrepresented in our database), including it in our analyses would obscure significant holes in our geographic and phylogenetic knowledge we feel are important to emphasize. We are confident that its exclusion does not change the patterns and biases as detailed in the main text.

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Chapter 3: Differential Trends in Primate Distributions Over Time Along an Elevational Gradient in Indonesian Borneo

3.1 Abstract

Predictions that primate populations will shift their range across space in response to environmental change are increasingly common. However, no study has empirically tested for or observed shifts in primate ranges, including along elevation gradients, the environments where shifts of tropical species are likely most feasible. Searching for these trends in dispersal-restricted species such as primates is crucial to validate model predictions, uncover the specific drivers of such changes, and identify the traits that are likely to mediate species' likelihood of shifting. We modeled the distribution of five sympatric primate species, three species over a 35-year period (*Pongo pygmaeus, Hylobates albibarbis, Presbytis rubicunda*) and two species over 20 years (*Macaca fascicularis, Macaca nemestrina*), across seven distinct habitats and a 5-1100 m.a.s.l. elevational gradient in Gunung Palung National Park, Indonesian Borneo. We found that all primates except *M. nemestrina* had declined in abundance over time. All five primates exhibited dynamic distribution trends along the elevational gradient, though sharp relative declines in the lowland peat swamp were consistent for all primates except *M. nemestrina*. Among all five species, the two ape taxa, *P. pygmaeus* and *H. albibarbis*, exhibited abundance trends most consistent with an uphill "lean" in their distributions. These similarities could reflect the roles of behavioral flexibility or home range size in mediating species' response to changes in

habitat quality. Our results indicate that signals of range shifts can be evident for long-lived species over relatively short time periods. However, given their overall abundance declines, shifting distributions may not be by itself a tractable strategy for these populations to avoid extirpation in the face of rapidly changing environments.

3.2 Introduction

Species distributions shift over space and time. Understanding how environmental conditions drive these dynamics is fundamental to discern the role of ecological factors (e.g. resource availability, climate) in both macro-evolutionary processes and the ranging patterns of extant species (Parmesan & Yohe, 2003). Knowledge of both informs predictions of whether modern populations can withstand rapid changes in their environments (Stewart et al., 2020).

Many species adaptively shift their distributions to track their preferred climatic niches. Ecological theory predicts that among terrestrial species, these shifts will trend polewards (to higher latitudes) and upwards (to higher elevations) as climate warms (Jonathan Lenoir & Svenning, 2013; Parmesan & Yohe, 2003; Rubenstein et al., 2023), a hypothesis that has been generally supported by species distribution modeling (SDM). SDMs are frequently employed to correlate species occurrences with environmental conditions across their entire geographic range and predict how occurrences will change as the abiotic environment changes (Dormann, 2007; Phillips et al., 2006, Winder et al., 2023). Observational studies have also described range shifts in modern populations for a broad array of terrestrial taxa including plants, insects, birds, amphibians, and small mammals, with many of these observed shifts following poleward or upward trajectories (Chen et al., 2011; Lenoir & Svenning, 2014; Freeman et al., 2018).

However, a surge in research on distribution shifts has complicated our basic understanding of this topic, especially on the smaller spatial scales most meaningful for

individual populations (Pearson & Dawson, 2003). First, there is increasing heterogeneity in which species and populations are shifting, and in which direction (Lenoir & Svenning, 2013; Pacifici et al., 2017; Tingley et al., 2012). A recent review found that in total, less than half of all observed range shifts across species have adhered to poleward or upward expectations (Rubenstein et al., 2023). Second, despite the high frequency of predictive models, tests of these predictions are rarely performed, even when "future" time scenarios have already passed (e.g. predictions for 2020: Luo et al., 2015). When models are tested, it is common for the observed shifts to be less frequent and smaller in magnitude than the models' predictions (Pacifici et al., 2017, Winder et al., 2023). Third, the structure of SDM's themselves may often preclude accurate predictions. Such limitations have been reviewed elsewhere (e.g. Santini et al., 2021, Winder et al., 2023), but include the frequent exclusion of biological factors such as species interactions (e.g. Ye et al., 2022), SDM's sensitivity to certain assumptions (Nenzén & Araújo, 2011), and lack of precision at smaller scales when models are based on macroclimate data (Maclean & Early, 2023).

Finally, our current insights into distribution shifts are based on a limited number of species and habitats; given that patterns in observed shifts have been highly species-specific (e.g. Pacifici et al., 2017; Tingley et al., 2012), limited taxonomic and geographic data preclude general conclusions about species' abilities to adapt to rapid environmental change. Our knowledge of distribution shifts in tropical systems is particularly limited (Beaudrot et al., 2018; Parmesan & Yohe, 2003; Rubenstein et al., 2023), even though tropical forests harbor most of the world's biodiversity (Gibson et al., 2011) and such forests are exposed to substantial environmental change (Brodie et al., 2011; Graham et al., 2016).

Primates are a keystone tropical taxon that may be particularly vulnerable to rapid environmental change (e.g. due to their slow life histories), yet our knowledge of primates on this subject is disproportionately low (Korstjens & Hillyer, 2016; Bernard & Marshall, 2020). This limits our ability both to reconstruct the role of environmental change in primate evolutionary histories, a field that often relies on lessons learned from modern analogues (Kingston, 2007), as well as our ability to inform management decisions for the conservation of extant populations.

Most studies that focus on primate distribution shifts use correlative SDMs. Consistent with other species, primate model results are quite species-specific, but in general primates' suitable habitat area and population sizes are projected to decrease as climate shifts (Bernard & Marshall, 2020; Winder et al., 2023). However, to date, no studies have reported observed range shifts in primates. There are two potential reasons for this. First, contemporary primate range shifts may not have been documented because they have yet to occur. Primate habitats are often quite fragmented and dispersal constraints such as geographic boundaries, lack of habitat corridors, and social behavior (e.g. territoriality) may impede primate species' ability to shift their ranges (Pinto et al., 2023; Schloss et al., 2012). Regardless of their ability to move, primates are also adaptable in other ways, and may for example take advantage of behavioral plasticity to adapt in place to new climatic conditions (Korstjens & Hillyer, 2016). Further, even though tropical species likely live close to their evolved temperature maxima (Tewksbury et al., 2008), perhaps the magnitude of climate change has not yet reached a threshold such that range shifts are advantageous.

Alternatively, contemporary range shifts in primates may be occurring, but are undocumented because they are difficult to track and observe. Indeed, there has only been one

published observation of contemporary range shifts in medium- or large- bodied mammals (Beaudrot et al., 2018). To describe such shifts, extensive time series data are required to distinguish true range shifts from short-term movements where individuals track seasonally favorable conditions (Lenoir & Svenning, 2013). Among mammals, primates have especially long life histories, and few multi-generational primate datasets are available (Beaudrot et al., 2018; Bernard & Marshall 2020). In the tropics, where climatic conditions are relatively homogenous, primates are unlikely to track latitudinal gradients as they would need to travel unrealistically long distances to encounter substantially different habitats (Loarie et al., 2009; Schloss et al., 2012). Elevation gradients, however, provide substantial habitat heterogeneity over short distances that primates may more feasibly exploit. Indeed, all SDM projections of contemporary primate range shifts occur along elevational rather than latitudinal gradients (Bernard & Marshall, 2020).

Studies of primates along elevational gradients offer particularly important perspectives on species' evolutionary history as well as the conservation of modern populations. Mountain slopes are likely critical refugia on evolutionary time scales (Colwell & Rangel, 2010) and thus act as an important influence on a suite of behavioral, morphological, and life history traits (Badyaev & Ghalambor, 2001). Similarly, on ecological timescales, we know little about the mechanisms by which elevational gradients may mediate a population's exposure to environmental change and impact its long-term viability. For example, contemporary climate shifts may be too rapid to sustain viable populations at higher elevations relative to the speed at which the habitat quality itself is changing, creating a "range-gap" between current and future distributions (Colwell et al., 2008). Upland forests may be a haven for modern populations should lowland habitats become uninhabitable and diversity in the lowlands crashes ("lowland

attrition": Colwell et al., 2008). Additionally, species already adapted to higher elevations may be prone to "mountaintop extinctions" if there are no separate populations in cooler conditions (Colwell et al., 2008; Malhi et al., 2010; Struebig et al., 2015).

Here, we investigate whether primates have undergone temporal distribution shifts at the Cabang Panti Research Station (CPRS) in Gunung Palung National Park, Indonesian Borneo. CPRS is characterized by multiple distinct habitats along an unfragmented, 5 – 1100 m.a.s.l. elevational gradient, and primate distributions have been monitored along the gradient since 1985. Specifically, we examine the distributions of the five most frequently observed primate species at CPRS, all of which are globally threatened species (IUCN, 2022): Bornean orangutans (*Pongo pygmaeus wurmbii*), Bornean white-bearded gibbons (*Hylobates albibarbis*), red leaf monkeys (*Presbytis rubicunda*), long-tailed macaques (*Macaca fascicularis*), and pig-tailed macaques (*Macaca nemestrina*). These primates live within all seven distinct forest types (described in detail below in the methods) found along the elevational gradient, with the exception of the two macaque species that are almost exclusively confined to the lowland forest habitats (see Marshall et al., 2014).

We have two primary goals: first, we assess whether habitat-specific abundances have changed over the last 35 years (since the beginning of data collection at CPRS), and whether these patterns are consistent across species. Second, we consider any apparent habitat-specific abundance trends in context, and ask if there are patterns that are consistent with an ongoing directional elevational shift (e.g., an upward shift may be indicated by decreasing abundance in the lowland habitats relative to increasing abundances in upland habitats). While this study is not a direct test of hypotheses that predict whether species will track their climatic niches along an elevational gradient, we aim to describe broad abundance patterns over time. These patterns will

be useful baselines for future work that can specifically examine the role of climate in shifting distributions.

3.3 Methods

3.3.1 Study site

Field research was conducted at CPRS in Gunung Palung National Park, Indonesian Borneo (1°13'S, 110°7'E). CPRS spans 34 km^2 and an 1105 m elevation gradient comprising seven distinct, contiguous forest types that differ in geology, soil type and drainage, forest structure, and plant species composition (see Fig. 1; Marshall et al., 2021). Forest types include the peat swamp (5-10 m.a.s.l.), freshwater swamp (5-10 m.a.s.l.), and alluvial bench (5-50 m.a.s.l.) in the lowlands, well-drained lowland sandstone (20-200 m.a.s.l.) and lowland granite (200-400 m.a.s.l.) forests, upland granite (350-800 m.a.s.l.), and montane forests (750-1100 m.a.s.l.) (Fig 3.1.; for more detailed description of forest types, see: Cannon et al., 2007a; Marshall et al., 2021). Due to CPRS's proximity to the coast, elevational zones are compressed (the Massenerhebung Effect: Grubb, 1977), resulting in substantial habitat differences over short spatial distances and the presence of true montane forests above 750 m.a.s.l. (Cannon et al., 2007a).

3.3.2 Data collection

Primate observations were collected at CPRS over 425 months between 1985-2020 by ML, AJM, ABB, and several teams of dedicated, highly proficient field assistants. Twelve vertebrate transects were originally established by ML in 1985 and were sampled continuously until 1992. These transects incorporated all seven habitat types, although sampling effort was

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Table 3.1. Total number of kilometers of transect walked by habitat in each period of data collection. Habitats are ordered by low-high median elevation for each period.

Period	Habitat	Total kilometers of transect walked
1	Montane	232.4
	Upland Granite	1776.55
	Lowland Granite	2210.6
	Lowland Sandstone	2906.25
	Alluvial Bench	3950.6
	Freshwater Swamp	2190.65
	Peat Swamp	1476.65
2	Montane	300.1
	Upland Granite	219.8
	Lowland Granite	194.25
	Lowland Sandstone	125.25
	Alluvial Bench	151.05
	Freshwater Swamp	143.05
	Peat Swamp	300.45
3	Montane	1818.7
	Upland Granite	3125
	Lowland Granite	2021.4
	Lowland Sandstone	1632
	Alluvial Bench	1655.85
	Freshwater Swamp	1330
	Peat Swamp	2219.65

skewed towards the lowland forests (Table 3.1). In 2000, AJM re-established and updated these transects into fourteen routes with mean length $3.4 \pm$ SD 0.24 km that were designed to equally sample all seven forest types (Nelaballi et al., 2022). These transects were monitored from 2000-2002 and from 2007-2020. In total, there were three primary periods of data collection at CPRS: 1985-1992, 2000-2002, and 2007-2020 (Periods 1, 2, and 3, respectively). Some census routes stayed within one habitat type, and others crossed multiple forest types. To attribute primate observations to their corresponding habitats, for transects spanning multiple forest types we separated each transect into "segments" by forest type for analysis. There were 32 total segments in Period 1 and 28 for each Periods 2 and 3, with segment lengths ranging from 50-3950 m.

Censuses began at 5:30 am (occasionally later during period 1), alternately starting at opposite ends to avoid potential biases associated with temporal variation in primate activity patterns (Marshall, 2004). Observers maintained a consistent walking pace of 0.75-1 km/hr, and censuses took on average 5-6 hours to complete. Usually one observer walked each census, but occasionally multiple observers participated (e.g. to train a new researcher). When a primate was spotted, observers recorded the species, group size (and their confidence in the observed group size), individuals' age and sex class, and estimated perpendicular distance from the first individual spotted to the nearest point on the census trail. For all three periods, we removed records that were most likely repeat observations of the same specific individual primate on a particular census. Except where otherwise noted, we only analyzed observations with complete group counts. Because this reduced our response variable sample size considerably, we reran all models including all encounters (those with complete and incomplete group counts) and found results consistent to those we report here.

We acknowledge that there were minor methodological differences in data collection among periods, but data collection protocols in periods 2 & 3 were designed to replicate those in period 1 and we do not believe there were any differences that would have systematically biased our results. Still, three discrepancies among data collection protocols deserve mention. First, during Period 1, researchers recorded count data on orangutans, gibbons, and leaf monkeys, but neither of the two macaque species. Second, we removed all identified "carried infants" from the Periods 2 and 3 datasets, as these individuals were not consistently recorded during Period 1. Third, census routes in Period 1 were surveyed with variable frequencies (mean = 5.19 ± 2.69 route replicates per month). Comparatively, in Periods 2 and 3 each route was walked consistently twice per month, with the exception of two montane forest routes that were not surveyed between 2012-2018. ABB re-initiated the monitoring of these routes between August 2019-August 2020 and increased the sampling effort from two to six replicates per route each month given the low probability of primate encounters in the montane forest (Marshall et al., 2014).

3.3.3 Analyses

3.3.3.1 Measuring elevation shifts over time

Range shifts can be measured by changes in a population's range margins, range core, or abundance (Lenoir & Svenning, 2014). While a "march" up- or down-slope would result from local colonization and extinction events at a species' dynamic *leading* or *trailing* range edges, "lean" shifts involve changes in abundance within stable range margins (the *front* and *rear* edges: Lenoir & Svenning 2013, 2014; see Fig. S3.1 for illustrative framework). Change in abundance is a particularly relevant measure for primate range shifts due to their stable home

ranges and long generation times that make marches along dynamic range edges less likely over relatively short periods.

We investigated primate distributions at CPRS using habitat type as categorical proxies for elevation rather than using elevation (e.g. measured in meters) directly. This way, an ongoing lean shift upwards, for example, would be indicated by a decrease in a species' abundance in lowland habitat types and a corresponding increase in the mid- or upland habitat types (see Fig. 1 in Beaudrot et al., 2018 for a conceptual visualization). As habitat type and elevation are highly correlated measures at CPRS, both could not be input as predictors in the same model (Fig. 3.1; Nelaballi et al., 2022). We chose to include habitat type rather than elevation in our models because the former has a greater influence than the latter on habitat quality and is known to affect primate group size, reproductive success, and probability of persistence (Marshall, 2010).

3.3.3.2 GLM modeling

We built generalized linear models to explore the effects of time and habitat type on primate counts. We assigned effort (measured in kilometers walked) as an offset variable to account for variable sampling regimes across periods. We represent time as a continuous integer grouped by 30-day sampling blocks (n = 261 blocks). We grouped censuses by 30-day period rather than month to standardize the duration of each sampling block. Sampling block integer values were centered on the mean and standardized (Gelman, 2008). For the habitat type categorical predictor, we set "peat swamp" as the reference category consistent with previous CPRS analyses (e.g. Nelaballi et al., 2022). We generated an interaction term between sampling block integer and habitat type to generate habitat-specific trends over time. Models also included a categorical effect for "period" to account for baseline differences in counts among periods.

Count data were overdispersed, thus all models were built on a negative binomial distribution using the function "glm" in the "stats" package in R (R version 4.2.2, R Core Team, 2022). Based on count estimates predicted by our models, we also calculated counts within a habitat type as a proportion of the total counts in that sampling block. We considered trends in these proportions over time as a measure of changes in primate dispersion patterns.

Two particular aspects of our model structure and interpretation merit acknowledgement. First, we do not model detection probabilities, and we report our results as a two-dimensional "counts per transect kilometer walked." Thus, we cannot directly compare our results with other reported primate densities (e.g. Marshall et al. 2014; Marshall et al., 2021), but we were restricted by minor methodological discrepancies among the periods. Because perpendicular sighting distances remained stable over time, we do not believe our results are biased, and we still accomplish our goal of comparing relative abundances across forest types through time. Further, we avoid the assumption of perfect detection that could more likely bias density estimates (Kellner & Swihart, 2014).

Secondly, predictors in linear models are commonly considered "reliable" when the 95% confidence intervals around their effect sizes do not overlap zero. Habitat-specific primate densities at CPRS are known to vary over short periods of time by orders of magnitude (e.g. (Marshall et al., 2009a; 2014; 2021). As such, particularly large confidence intervals around effect sizes are unsurprising and accurately reflect observed spatiotemporal fluctuation in primate densities. To account for this, we looked for patterns and changes in full confidence intervals across forest types, even if an interval overlapped zero (see Fig. S3.1).
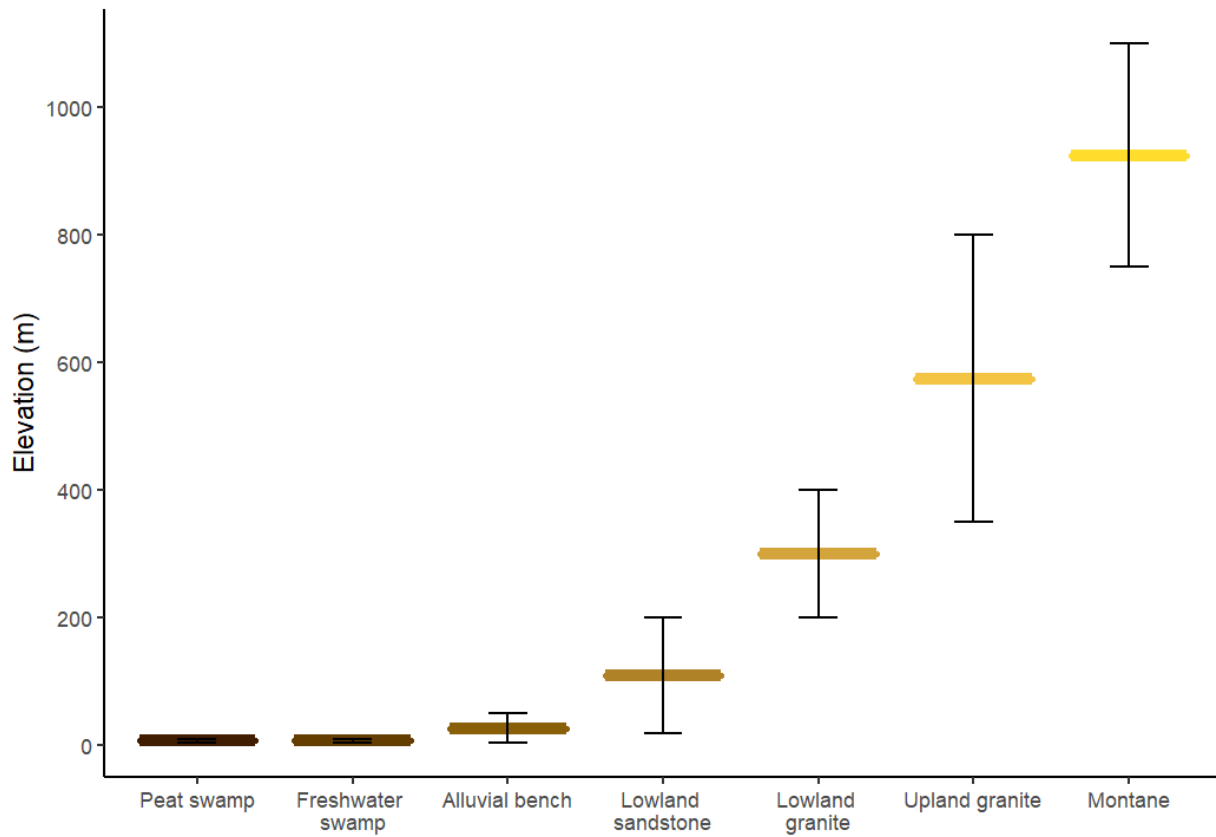
Figure 3.1 Median elevation of the seven forest types (with low and high range values specified) at Cabang Panti Research Station. See Marshall et al., 2021 (Fig. 1) for a map of the census trail system across these forest types.

3.4 Results

3.4.1 Long-term average habitat preferences across primate species

Baseline differences in species' abundance varied substantially across habitat types, consistent with previous investigations of primates at CPRS (Fig. 3.1; Marshall et al., 2014). Long-term averages indicate that the highest mean abundance of orangutans is found in the peat swamp (average counts per kilometer of transect walked = 0.109 ± 0.126 SD), the freshwater swamp for pig-tailed macaques (0.0350 ± 0.223), alluvial bench for leaf monkeys (0.456 ± 0.464) and long-tailed macaques (0.720 ± 0.699), and lowland sandstone for gibbons (0.414 ± 0.457) (Fig. 3.2). All primates were observed in all forest types except for long-tailed macaques, which were observed in neither the upland granite nor montane forests. While long-tailed macaques were present in the lowland granite forest, there were only two encounters with individual primates since 2000; thus, the lowland granite forest type was excluded from that species' models. Additionally, while pig-tailed macaques were observed in all seven forest types, there were only four independent observations above the lowland granite forest; thus, the two upland forest types were excluded from that species' analyses as very low counts prevented model convergence.

3.4.2 Changes in abundance over time

3.4.2.1 Overall abundance trends

Models estimating counts of primates over time indicate that all primate abundances except pig-tailed macaques are in decline at CPRS (Fig. 3.3). Between 1985 and 2020, the odds

of counting a primate on a transect decreased by 0.203 (± 0.26 SE) for orangutans, 0.202 ± 0.20 for gibbons, and 0.380 ± 0.22 for leaf monkeys. Between 2000 and 2020, the odds of counting a long-tailed macaque on a transect decreased by 0.693 ± 0.20 and increased by 1.321 ± 0.55 for pig-tailed macaques. The wide confidence intervals for the pig-tailed macaque estimate indicate that the trend in counts is not reliably positive; nevertheless, it was the only species for which counts did not reliably decrease over time.

3.4.2.2 Differential abundance trends by habitat

When forest type is added as a predictor of primate counts, differential occurrence trends over time across those forest types are evident (Fig. 3.4). For four of the primate species, abundance trends in the peat swamp are distinctly negative relative to all other habitats: there were decreased odds (i.e. the effect size is less than 1 on an odds scale) of observing orangutans over time in the peat swamp by 0.178 ± 0.285, 0.103 ± 0.235 for gibbons, 0.149 ± 0.276 for leaf monkeys, and 0.188 ± 0.618 for long-tailed macaques.

Abundance trends across other habitats are more species-specific, but orangutans and gibbons share some noteworthy trends. Comparing counts in the two lowland swamp habitats with the three highest-elevation habitats, the odds of counting orangutans and gibbons below 10 m.a.s.l. in freshwater swamp (0.103 ± 0.235 and 0.149 ± 0.276, respectively), are declining distinctly more than the odds of counting individuals of those species above 350 m.a.s.l. in the upland granite (orangutans: 0.923 ± 0.214, gibbons: 2.305 ± 0.184) and montane forests (orangutans: 1.192 ± 0.729, gibbons: 4.219 ± 0.654). Trends in leaf monkeys did not vary as much over space, as the relative odds of counting individuals over time freshwater swamp (1.796 ± 0.213) overlapped substantially with odds in the lowland granite (2.207 ± 0.209) upland granite (2.458 ± 0.220) and montane forests (2.063 ± 0.523).

It is possible that apparent differences along the elevation gradient as a whole may be skewed by disproportionate declines in the swamps. Therefore, we reran the models excluding both lowland swamp habitats. Because forest types in the lowlands are more compressed and have tighter elevational ranges relative to the upland habitats, these models retained the majority of CPRS's full elevational gradient (Fig. 3.1). The results of these models are not substantively different than the trends predicted by the full model: abundance trends of orangutans, gibbons, and leaf monkeys were the most negative in the alluvial bench (now representing the lowest-elevation habitat), relative to other habitat types, and trends in the highest elevation habitats remained increasingly positive for orangutans and gibbons (Fig. S3.2).

Among all forest types, gibbon relative abundances increased the most in the two upland forest types (Fig. 3.4). In contrast, the two most positive relative abundance trends for orangutans (odds of 1.26 ± 0.170 and 1.42 ± 0.181) and leaf monkeys (3.42 ± 0.191 and 2.91 ± 0.198) occurred in the alluvial bench and lowland sandstone habitats, respectively, while the two most positive abundance trends for long-tailed macaques were in the freshwater swamp (4.45 ± 0.649) and alluvial bench (4.13 ± 0.625).

In general, encounters of long-tailed macaque groups (n = 463 total group encounters) were lower than the other three species (n = 3385 gibbon group encounters, 3141 for leaf monkeys, and 1474 for orangutans), and pig-tailed macaque group encounters were far lower (n = 72). Thus, disparity in sample sizes likely contributed to decreased confidence around our models' estimates of relative abundance trends across forest types (Fig. 3.4). However, overall, both macaque species were consistent with red leaf monkeys in showing high overlap in abundance trends among forest types, and no discernable directional signal along the elevational gradient.

3.4.3 Changes in dispersion over time

Proportional dispersion patterns in primates' use of space can indicate trends distinct from abundance changes. For example, even while orangutans show sharp declines in abundance in the peat swamp over time, the counts of orangutans in the peat swamp as a proportion of total counts across all habitat types remains remarkably even (a 1.9% increase in proportional occupancy over time; Fig. 3.5).

Between 1985 and 2020, the proportion of counts in the upland granite forest was relatively stable for orangutans (1.87% to 2.57%) and leaf monkeys (3.08% to 2.66%), while the proportion of gibbon counts nearly doubled (7.57% to 12.20% of observations). Similarly, in the montane forest, proportions of sightings adjusted for effort were relatively constant for orangutans (8.16% to 7.18%) and leaf monkeys (10.97% to 12.12%), while the proportion of gibbon sightings nearly quadrupled (0.73% to 2.77%).

In the lowland forests, the proportion of counts of orangutans declined by half in the freshwater swamp to 12.12%, with the second-highest proportion of counts after the peat swamp shifting upslope to the alluvial bench (20.8%) and lowland sandstone (19.8%). For gibbons, counts declined by over 50% (23.3% to 11.62%) in the peat swamp and almost 50% in the freshwater swamp (19.6% to 10.5%), while proportions increased upslope in all other habitats, particularly the lowland sandstone (19.9% to 27.9%). For leaf monkeys, the proportion of counts in the peat swamp in 2020 were less than a third of what they were in 1985 (18.2% falling to 5.7%) and declined in the freshwater swamp from 19.8% to 14.1%, while proportions almost doubled in the upslope alluvial bench (16.0% to 28.0%) and increased in the lowland sandstone from 15.7% to 22.0%.

Trends in proportions of counts over time for macaque species were particularly wide-ranging, likely due in part (as previously mentioned) to smaller sample sizes. The proportion of long-tailed macaques started off highest in the alluvial bench (41.9%) and climbed even higher over time (59.2%), while proportions in both the upslope lowland sandstone and the downslope peat swamp dropped precipitously over time (31.0% to 6.1% in the lowland sandstone, and 6.4% to 0.5% in the peat swamp). Observations of pig-tail macaques were proportionally highest in the lowland sandstone in 1985, but over time observations in that habitat crashed to 4.2%. Simultaneously, proportions of counts began lowest in the freshwater swamp (1.7%), but surged to 49.5% of counts over time, representing the habitat with the highest proportion of observations in 2020.
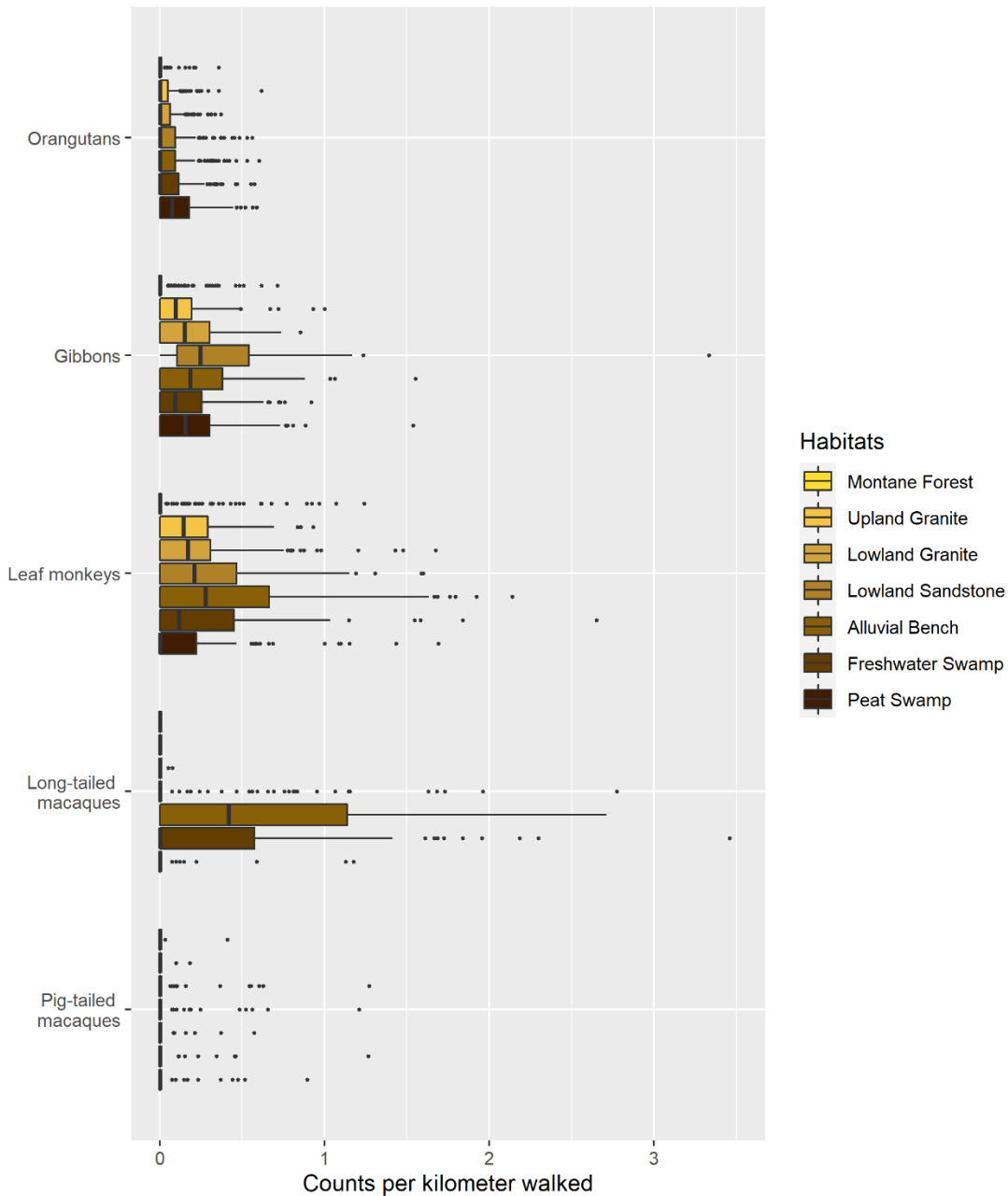
Figure 3.2. Spatial variation in counts of independently-traveling primates adjusted for effort. Each row represents individual counts in a distinct habitat type, and for each primate are ordered by increasing elevation. Boxplots indicate the middle 50% of observations, and the median value is indicated by the solid black vertical bar. To increase plot legibility, we limited the x-axis to 3.5 kilometers walked, which cut off three outlier points from the plot: one point of 4.71 gibbons per km in the Lowland sandstone habitat, one point of 4.44 gibbons per km in the Lowland granite habitat, and one point of 3.69 leaf monkeys per km in the Peat swamp.
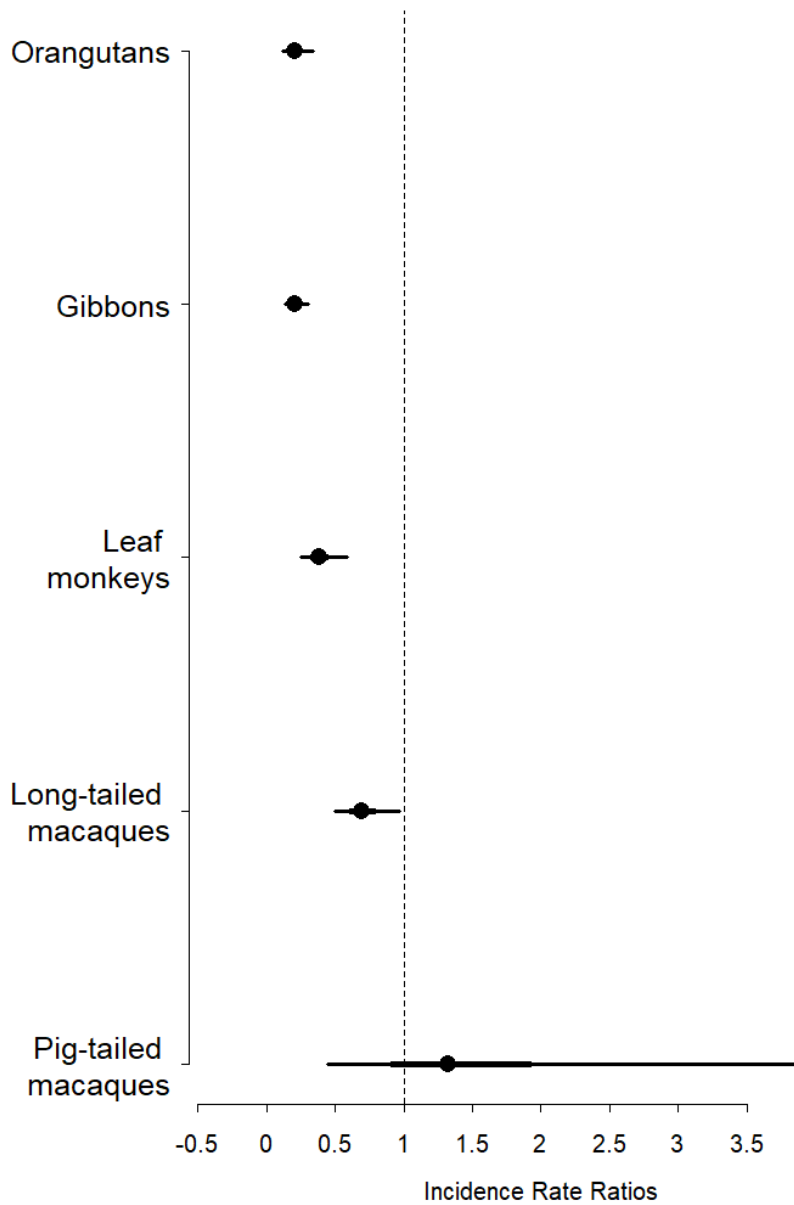
Figure 3.3. Back-transformed (exponentiated) beta coefficients indicating the odds of counting primates over time. Points to the left of the dotted line at an odds ratio = 1 indicate decreasing odds of counts as time increases, i.e. a negative effect of time. Lines represent 95% (thin) and 50% (thick) confidence intervals around the maximum likelihood estimate for each effect. Models also included the period of data collection as a categorical variable, but only coefficients for time are shown.
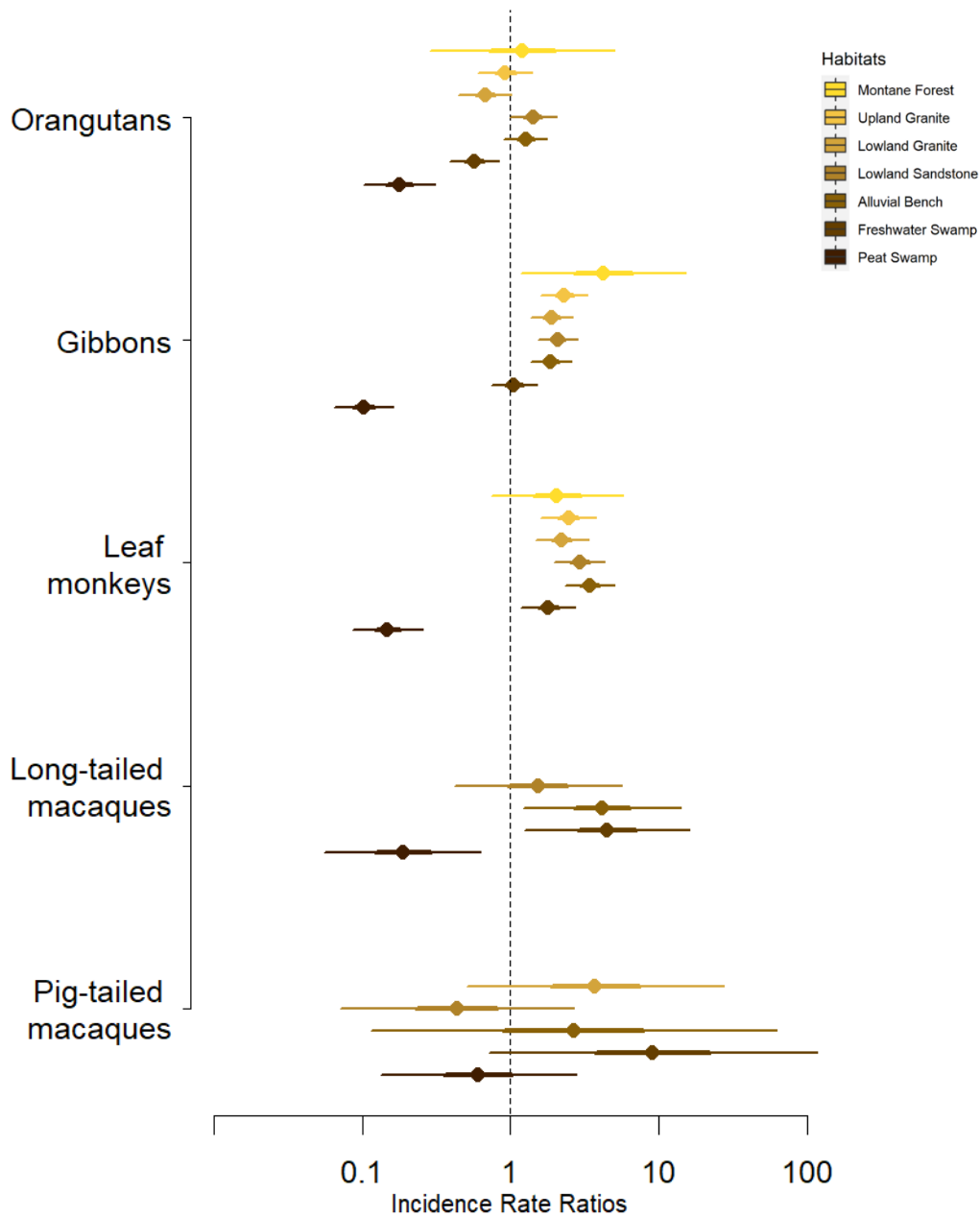
Figure 3.4. Back-transformed beta coefficients indicating the effect of time on primate counts conditioned by forest type. Lines represent 95% (thin) and 50% (thick) confidence intervals around the maximum likelihood estimate for each effect. Habitat types are organized by increasing elevation for each primate, as in Figure 3.2. Habitat colors are also consistent with Figure 3.2 (e.g. dark brown represents low-elevation peat swamp, and light yellow represents high-elevation montane forest).
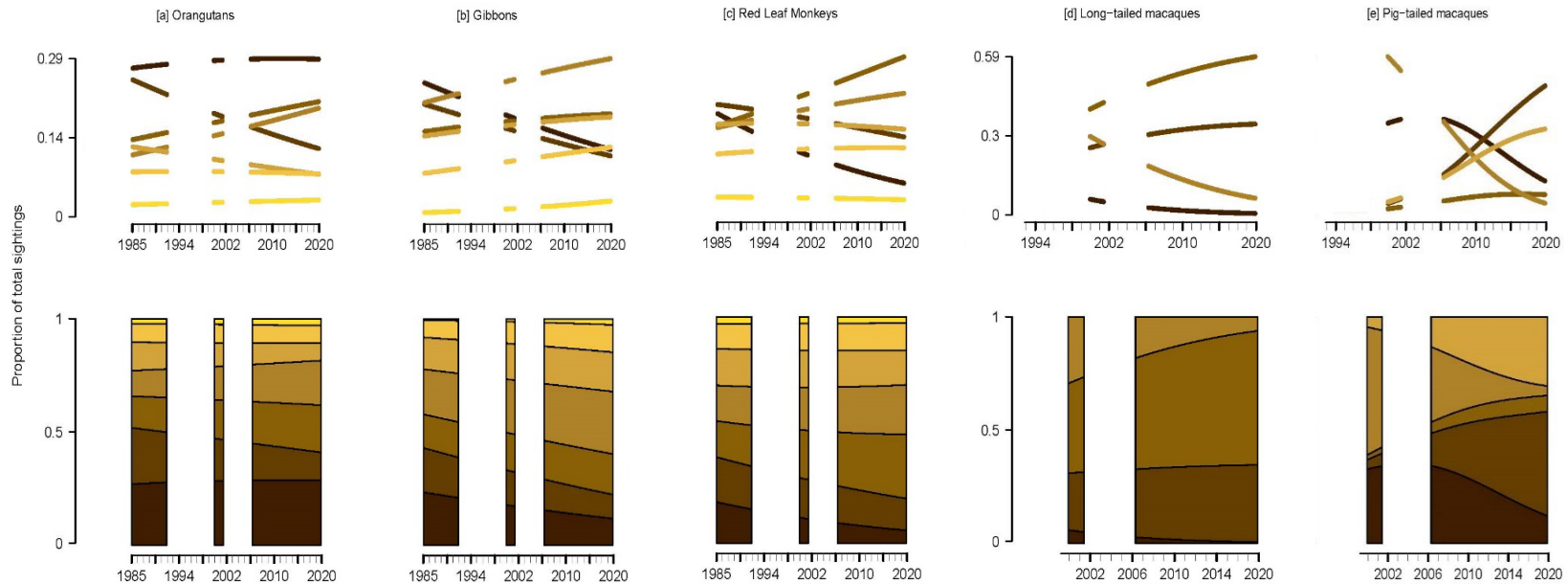
Figure 3.5. Dispersion dynamics of orangutans [a], gibbons [b], leaf monkeys [c], long-tailed macaques [d], and pig-tailed macaques [e] at Cabang Panti Research Station. Habitat color scheme matches Figures 3.2 and 3.4. For each primate, the top row indicates trends in proportion of total counts for each species across forest types as predicted by count models. The bottom row plots those proportions as a grouped barchart, and habitat types are ordered by increasing elevation. Note that the y-axis scale is different for panels [a], [b], and [c] than for [d] and [e], and the total number of counts for [d] and [e] are calculated based on a different time series (beginning in 2000, rather than 1985) and fewer than seven forest types.

3.5 Discussion

Our investigation of long-term distribution dynamics of five sympatric primate species represents the first observational study in support of widespread predictions that environmental change will drive primates uphill. Observations of such range shifts for any medium-large bodied mammal are scarce (Beaudrot et al., 2018). While we report one of the longest-duration studies of sympatric primate populations to date, 35 years remains a short timeframe relative to the lifespan of individual primates. For example, orangutan generation time is estimated to be ~20-25 years (Hobolth et al., 2007; Hobolth et al., 2011), thus 35 years likely represents fewer than two full generations. Yet, our findings indicate that even long-lived species can demonstrate population-level signals consistent with ongoing range shifts over relatively short periods of time.

Below, we describe the specific features of primate ranges that are changing, and how these results support the general predictions of climate-induced range shift theory. We then identify three possibilities for why the distribution patterns of orangutans and gibbons resemble each other more closely than the three Cercopithecine species in our study. We explore our results in light of additional potential environmental drivers, identify potential sources of bias in our analyses, and outline several crucial topics that subsequent studies can address.

3.5.1 Some primates indicate leans upslope

All five focal primate species at CPRS exhibit distribution patterns that are dynamic through space and time. Some of these trends are consistent with an upwards "lean" as distributions shift within stable range boundaries. Such "lean" shifts are more likely over short time scales for long-lived, large-bodied species that may only alter their range boundaries

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("marching" shifts) on longer time scales (Maggini et al., 2011; Rubenstein et al., 2023; but see Beaudrot et al., 2018).

3.5.1.1 Retractions from rear edges

Notably, the abundance of all focal primates is declining in the peat swamp, the low elevation "rear edge" of their range. These declines are particularly concerning for orangutans, a species that relies on the peat swamp as a fallback habitat when food in preferred habitats is scarce (Marshall et al., 2021). Dispersion trends also indicated that the proportional abundance of primates in low elevation habitats has either remained stable or declined over time, with counts of orangutans, gibbons, and leaf monkeys proportionately all decreasing in the peat freshwater swamp and gibbons and leaf monkeys proportional declining in the peat swamp as well.

While rear-edge declines were particularly evident across species as abundance declines in the peat swamp, the same rear-edge effect was detectable when we removed counts in the swamps from analysis and limited species' rear edges to the alluvial bench habitat (Fig. S3.2). This consistency further supports the likelihood of a true elevation effect over time, rather than patterns that resemble rear-edge effects but are solely driven by a particularly large effect in the peat swamp.

3.5.1.2 Increases at front edges

Concurrent with rear-edge trends, there were indicators of abundance leans towards the high-elevation "front edge" of some primates' ranges. Unsurprisingly, given they are poor quality habitat for all three species, proportional occupancy of the upland granite and montane forests was low for orangutans, gibbons, and leaf monkeys. In contrast, for these species, the proportionate use of upland habitats either remained stable or increased over time. Gibbons and

orangutans in particular showed differential changes in their abundance across habitats that generally become less negative—or even positive—for these primates as elevation increased (except for the transition between the lowland sandstone and lowland granite habitats: Fig. 3.4). Also, the most positive relative abundance trends for gibbons occurred in the two highest elevation habitats.

Finally, while we excluded pig-tail macaque observations above the lowland sandstone from our models because of very small sample sizes, we note that three of the four pig-tailed macaque observations in upland forests occurred in either 2019 or 2020. These observations, though isolated, offer a preliminary sign that the front edge of their range is dynamic and expanding upwards over time (Lenoir & Svenning, 2013).

3.5.1.3 Shifts in core habitats

The forest type with the highest abundance for each primate species was either stable over time, or shifted to a higher-elevation forest type. In particular, the two habitats for which the proportional counts of gibbons and leaf monkeys were highest all shifted in each species to a higher-elevation habitat over time, as well as the habitat with the second-highest proportion of orangutans (Fig. 3.5).

Such changes may indicate true ongoing shifts in species' core habitats, representing changes in areas where primates' growth and fitness are most enhanced. Alternatively, these patterns could represent a by-product, rather than a driver, of general abundance declines: if external drivers cause overall primate abundance to decrease and key high-quality habitats (e.g. alluvial bench, lowland sandstone) are no longer at carrying capacity, then primate groups in relatively poor-quality habitats (e.g. the peat swamp) might preferentially migrate to those higher quality habitats at slightly higher elevations.

3.5.2 The potential role of climate as a driver

Changes in primate distributions at CPRS are occurring simultaneously with trends in the regional climate: land surface temperatures on Borneo as assessed from remote sensing data are warming and precipitation is generally declining (Kumagai et al., 2013). Some of the greatest temperature increases on Borneo in the last two decades have occurred specifically in West Kalimantan, the province where CPRS is located (Munawar et al., 2022). In light of these regional trends, our results provide the first empirical support for the longstanding hypothesis that contemporary climate changes will drive primates uphill. However, given that most primate populations at CPRS are in decline, our results are also consistent with indications that primate niche evolution is vastly outpaced by the contemporary climate changes themselves (Meyer & Pie, 2021), suggesting that range shifts along elevational gradients may be inadequate to ensure persistence in the face of rapid climatic change (Parmesan, 2006).

3.5.3 Examining effects of behavioral flexibility, territory size, and habitat quality

In general, the distribution patterns of gibbons and orangutans are more consistent with each other, and most closely resemble an uphill lean, than the three cercopithecine primates at CPRS. As apes, gibbons and orangutans are generally characterized by their large relative brain size and substantial evolved behavioral flexibility (van Schaik, 2013), and gibbons and orangutans may be more capable than other primates at CPRS of modifying their behavior in response to changes in their environment. For example, apes could reduce thermal stress from increasing temperatures by resting more (Korstjens et al., 2010). Over a long period, this strategy could suit apes better than smaller-bodied primates, whose quicker metabolic rates would not enable them to sustain long durations of negative energy balance. Enhanced behavioral

flexibility, however, would suggest that apes would be less likely than other primates to exhibit a range shift, and more likely to adapt in place. Therefore, we explore two alternate possibilities why these species may more closely resemble patterns associated with range shifts.

One possibility highlights a potential methodological consequence of increased resting time in these species. Decreased activity levels could correlate with a decreased likelihood of observing these primates on census tracts. If true, this could disproportionately affect gibbons and orangutans: their smaller group sizes and preference for higher levels of the canopy than other primates (Marshall 2010; Cannon & Leighton, 1994) may increase the difficulty of spotting individuals while they are inactive. If warming temperatures in lowland habitats disproportionately cause increases in resting behavior relative to upland habitats, that may decrease the probability that individuals are observed on lowland habitat censuses relative to upland habitats where temperatures are cooler. In this scenario, our models would have overestimated their overall abundance declines.

A second possible explanation for similarities in gibbon and orangutan abundance trends is based on species traits for which orangutans and gibbons are noticeably different, rather than alike. The fundamental assumption of range shift predictions is that species travel uphill as the relative quality of lowland habitats decreases in concert with a relative increase in quality of upland habitats. The ability of primates to track these changes in habitat quality, however, is restricted by their social behavior. In particular, differences in species' territory sizes and the degree to which they aggressively defend those territories may impact whether the habitat-specific abundances of primates change over time, and what the observed changes actually indicate.

Specifically, we may observe a range-shift signal in orangutans because individuals have very large territories (ca. 508 ha. at CPRS: Knott et al., 2008) and can cover great distances across habitats to track spatiotemporal fluctuations in their food (Leighton & Leighton, 1983; Marshall et al., 2021). If, for example, there is on average increasing food availability in the uplands, orangutan individuals may occupy those habitats more frequently relative to the lowland habitats that have proportionately decreased in quality. To that end, the overall decline in counts of orangutans at CPRS may ultimately indicate that individuals are increasingly traveling outside the boundaries of the CPRS trail system. In contrast, gibbons have particularly small territory sizes (ca. 43 ha at CPRS: Marshall, 2004) that groups aggressively defend, both traits that severely restrict individuals' ability to disperse. Thus, a range shift would be evident if increasing food availability in the uplands slowly increases the gibbon carrying capacity of these forests relative to the declining carrying capacity in the lowlands. In this scenario, decreases in counts of gibbons at CPRS would more likely indicate true declines in their CPRS population, unlike orangutans.

Variation in species' territorial behavior could also explain the increased overlap in habitat-specific abundance trends over time observed in leaf monkeys and both macaque species. The average territory sizes of leaf monkeys at CPRS are over twice as large (ca. 90 ha.: Marshall, 2004) as gibbons, and are therefore on average more likely to span multiple habitats. This increases the probability that specific leaf monkey groups can cross habitat boundaries, but not consistently enough to register the habitat-specific trends of orangutans. Simultaneously, leaf monkeys maintain a wide diet breadth and can fall back on very abundant leaves when preferred food availability is low (Marshall et al., 2009a), indicating that any change in the qualities of their habitats may not synchronize at all with the factors that affect other frugivorous primates.

While home range dynamics of macaque species at CPRS are less well-studied, the home range of one long-tailed macaque group at CPRS was estimated at 200 ha. (Lawrence, 1989), and pig-tailed macaques elsewhere on Borneo average 300 ha. home ranges (Nunn & van Schaik, 2002). Like leaf monkeys, these ranges are larger than gibbons but smaller than orangutans. The increased variability in the estimates around their habitat effects, while in part a function of smaller sample sizes of observations, also indicates that groups may be more flexible in their movements across space. Biologically, this flexibility could be facilitated by their large home ranges as well as relatively high tolerance of overlapping territories with other groups (Lawrence, 1989; Oi, 1990).

3.5.4 Other potential drivers of distribution dynamics

Although our models support the hypothesis that climate may drive some primate distributions uphill, that does not solidify climate as a driver of these trends. Indeed, regional approximations of land surface temperatures may not precisely reflect primates' local environments at all. For example, canopy cover is known to insulate the forest interior, with understory microclimate temperatures either cooler or warmer than the ambient air temperature depending on specific conditions (De Frenne et al., 2019). In Borneo, these effects persist despite canopy thinning driven by selective logging (Senior et al., 2017).

In addition to climate, there are a host of other anthropogenic factors known to affect extant primate distributions, all of which may interact with climate or each other to affect species in complex ways that remain difficult to measure (Brodie, 2016; Mantyka-Pringle et al., 2012). Habitat loss is the single most pressing driver of primate decreases worldwide (Estrada et al., 2017), and the forests in Indonesian Borneo alone decreased by 70% between 1973 and 2010 (Gaveau et al., 2014). Deforestation disproportionately impacts lowland forests relative to upland

forests (Struebig et al., 2015), and over time, the deforested area immediately surrounding Gunung Palung National Park has grown larger (Zamzani et al., 2009). CPRS itself was closed between 2002-2006 due to escalating tensions with loggers in communities outside of the National Park boundary beginning in 2000 (Dillis et al., 2018). Proximity to logging villages is known to decrease primate abundance and occupancy elsewhere on Borneo (e.g. Cheyne et al., 2016; Marshall et al., 2005), and may contribute to the high rates of decline from lowland forests at CPRS.

Forest fires are a particularly dominant cause of habitat loss on Borneo, and directly devastate large tracts of primate habitat with long-term consequences for large mammal occupancy (Cheyne, 2008). Regionally, peat swamps are disproportionately burned relative to other forest types (Page et al., 2009), although the peat swamps within the National Park boundary have not burned over the duration of the study period. Smoke from fires can also indirectly bring about many short- and long-term fitness consequences (e.g. adverse health effects of smoke inhalation: [Koplitz et al., 2016], obscuring food availability for sight-dependent foragers [Harrison et al., 2016], decreasing food production [Davies & Unam, 1999], leading to negative energy balance [Ashbury et al., 2022; Erb et al., 2018] and reproductive behavioral changes [Cheyne, 2008; Ashbury et al., 2021]). While smoke travels great distances and extends far up into the air column, it is possible that the negative effects of smoke are reduced at higher altitudes where stronger prevailing winds could clear away smoke more rapidly.

Hunting, whether for bushmeat or the pet trade, is another prevalent driver of primate declines worldwide (Estrada et al., 2017) and in Borneo (e.g. Cheyne et al., 2016). In eastern Borneo, orangutan densities decreased as proximity to villages known to hunt orangutans

decreased (Marshall et al., 2006), and some communities surrounding Gunung Palung National Park are known to hunt primates (Johnson et al., 2005). Thus, it is possible that hunting may partially explain rapid rates of primate decline in the lowland forests closer to the edge of the National Park. On average, it is likely that hunters have disproportionately targeted lowland forests regardless, where baseline vertebrate densities are generally higher (this study, Fig. 3.2; Marshall et al., 2014).

Habitat disturbance also facilitates encroachment from rapidly-colonizing invasive species that can dramatically impact biodiversity and native ecosystem functions (Sax & Gaines, 2008). At CPRS, the invasion of *Bellucia pentamera* may be uniquely impactful for primate populations. This invasive Neotropical tree began to naturalize around CPRS in the early 2000s, where it quickly became established just outside the protected area in forest gaps created by heavy selective logging in peat swamp habitats (Dillis et al., 2015). It produces large crops of fruit that all primates eat, and it fruits more frequently than any known native plant (Dillis et al., 2018). This combination of factors could draw primates away from the study site where food is consistently scarce outside of short-term supra-annual masting events (Cannon et al., 2007b). For primates that are both behaviorally restricted from dispersing large distances, those in groups that inhabit lowland edge habitats most proximate to logged forest patches may be disproportionately drawn out to such patches where *Bellucia* are most abundant.

3.5.5 Limitations and potential sources of error

There are several reasons to interpret our findings with caution. First, we derive abundance estimates from visual observations of primates on standardized census routes. Census transects are a staple method of ecological monitoring but may over-represent counts if certain events increase the probability that primates will be observed in subsequent censuses, such as

individuals returning to a fruiting tree. In general, these effects should be minimized by offsetting the sampling of each census route by two weeks. However, this offset was not standardized until Period 2, and more concentrated sampling sometimes occurred during Period 1. Census routes during Period 1 disproportionately sampled lowland forests relative to upland forests, but we included sampling effort as an offset term in our models to minimize the risk that this skew meaningfully biases abundance estimates.

Relying on visual observations of study subjects may underestimate the range of ecological variation primates can tolerate (Araújo & Pearson, 2005), a key consideration in environments where primate densities are naturally low. Some primates are more secretive than others (e.g. pig-tailed macaques), and estimates of gibbon densities in particular may be underestimated when derived from visual census data compared with acoustic surveys (Gilhooly et al., 2015). However, given that our primary goal was to compare relative trends across space, rather than develop precise total population estimates, we believe that such biases should minimally impact our results.

Finally, habituation rates of primate groups may vary by species and over space. For example, gibbons travel high in the canopy and may habituate to human presence slower than long-tailed macaques that prefer lower canopy levels (Cannon & Leighton, 1994). Primates living in habitats at lower group densities may also habituate slower than groups that live at higher densities, as on average any given group is exposed to less human interaction. Despite this, distribution trends at CPRS are unlikely to be driven by habituation effects, as the dominant effect of habituation over time would be to increase rather than decrease estimated abundances.

3.5.6 Additional priorities for future research

A critical next step in investigating distributional changes in primates along elevational gradients is identifying the causal mechanisms of these trends. We have hypothesized that climate may be among these drivers at CPRS, although this finding relies on an assumed association between regional climate indicators and the environmental conditions actually experienced by primates. Primates are known to modify their behavior in response to microclimate conditions within tropical forests (Takemoto, 2004), and future studies would benefit from explicitly examining whether local weather patterns reflect broader climatic trends.

Regardless of whether climatic changes are driving these distribution patterns, fundamental questions remain about the nature of how primate distributions are related to their environments. Specifically, do observed distribution patterns through time directly reflect changes in their abiotic environment, or are changes more impactful as they are mediated through effects on primates' biotic environment? Forest types at CPRS are distinct in more ways than their elevations, and biotic attributes including forest structure, floristic composition, and plant reproductive phenology (Marshall et all., 2014) are known to influence habitat-specific primate carrying capacities (Marshall 2010). Some biotic metrics have been shown to change over time due to climate, including declines in food availability [Chapman et al., 2010; Potts et al., 2020] and decreasing food quality [Rothman et al., 2015]). Hypothetically, general declines in abundance as indicated by our analysis would make mathematical sense in a scenario in which the quality of lowland habitats is declining quicker than increasing quality of upland habitats can compensate. Thus, investigating whether and how species-specific metrics of habitat quality have changed over time is crucial.

Many projections of primate distributions along elevational gradients rely on direct links between primates and abiotic conditions (e.g. Luo et al., 2014), and threshold effects of

temperature can have drastic effects in other wild mammalian populations (Welbergen et al., 2008). At CPRS, rain and low temperatures were each found to negatively impact orangutan abundance in upland forests, likely due to thermoregulatory constraints (Marshall et al., 2021). Relatedly, the montane forests into which gibbons are proportionately expanding are a sink habitat that lacks figs, their most important fallback food (Marshall, 2009), suggesting that factors other than food availability are responsible for their lean upslope.

Finally, we have modeled all primate distributions independently, thus assuming that species have no impact on each other's distributions. However, biotic interactions among species are known to impact ecosystem dynamics, particularly in the tropics where species diversity is high (Post 2013). In Kibale National Park, chimpanzee hunting was determined to be the key driver of long-term population declines in red colobus monkeys (Chapman et al., 2023). While no such predator-prey interactions characterize inter-primate relationships at CPRS, competition over food may be more relevant: for example, the diet of gibbons at CPRS overlaps by at least 40% with leaf monkeys, long-tailed macaques, and orangutans, as well as Prevost's squirrels (*Callosciurus prevostii*) (Marshall et al., 2009b). Such high dietary overlaps may contribute to negative correlations among the distributions of same five species of primate in a forest in East Kalimantanw (Rodman, 1979). While studies at CPRS have not found similar negative correlations in species' densities across space (Marshall et al., 2009b, Marshall et al., 2014), there are two caveats to these results. First, these analyses were restricted to data over shorter intervals than the current study. Thus, they could not account for the potential long-term changes in habitat quality over time, and the potential for concurrent changes in inter-species relationships themselves. Secondly, their use of space compared abundances of primates across

habitat types, whereas negative correlations could apply on a finer-grained scale within a forest type.

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3.7 Supplemental Information
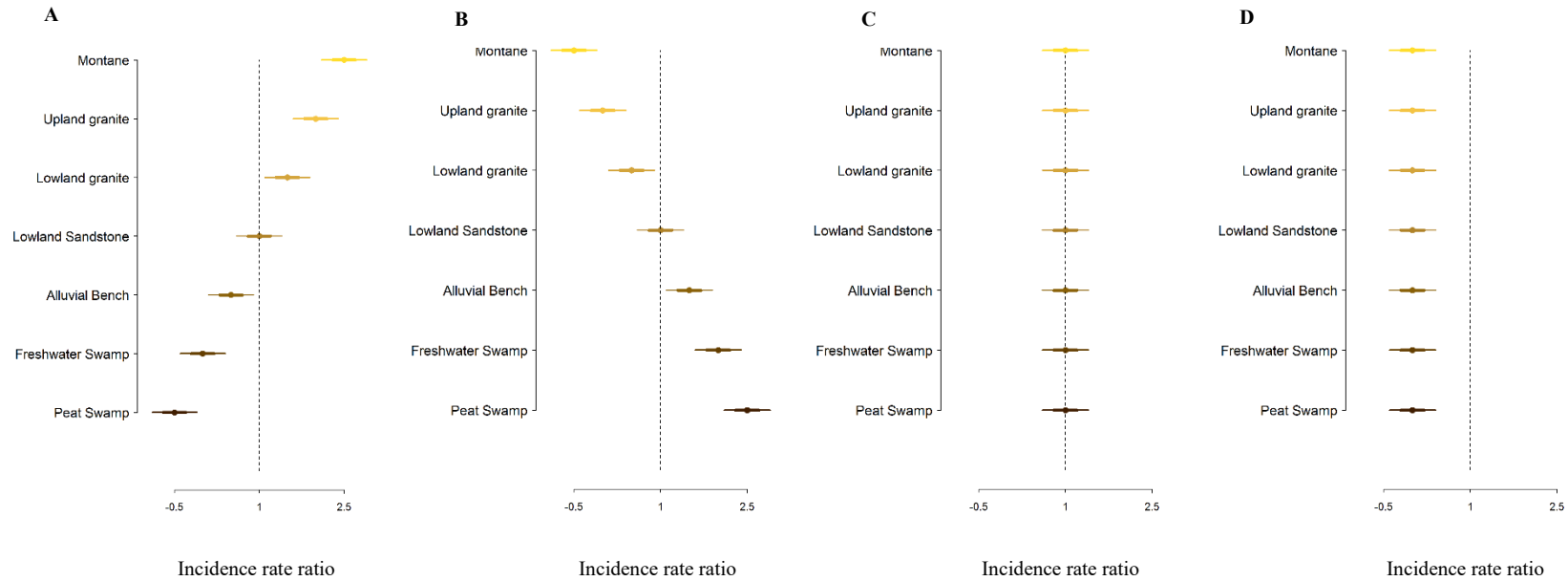
Figure S3.1. Framework for visualizing distribution shifts as effects in a coefficient plot. Elevation increases from bottom to top. [A] shows a hypothetical upwards lean: relative abundance is decreasing the most in the lowest elevation habitat, and increasing the most in the highest elevation habitat. [B] shows a hypothetical downwards lean, with relative abundance decreasing the most in the highest elevation habitat and increasing the most in the lowest elevation habitat. [C] represents a population with no overall abundance change over time and no effect (or influence) of elevation, as all the habitat-specific beta coefficients and their confidence intervals are overlapping. [D] represents a population that is decreasing, as all habitat-specific beta coefficients are negative, but there is still no effect of elevation as all beta coefficients are overlapping (the abundance decreases are equal along the elevational gradient).
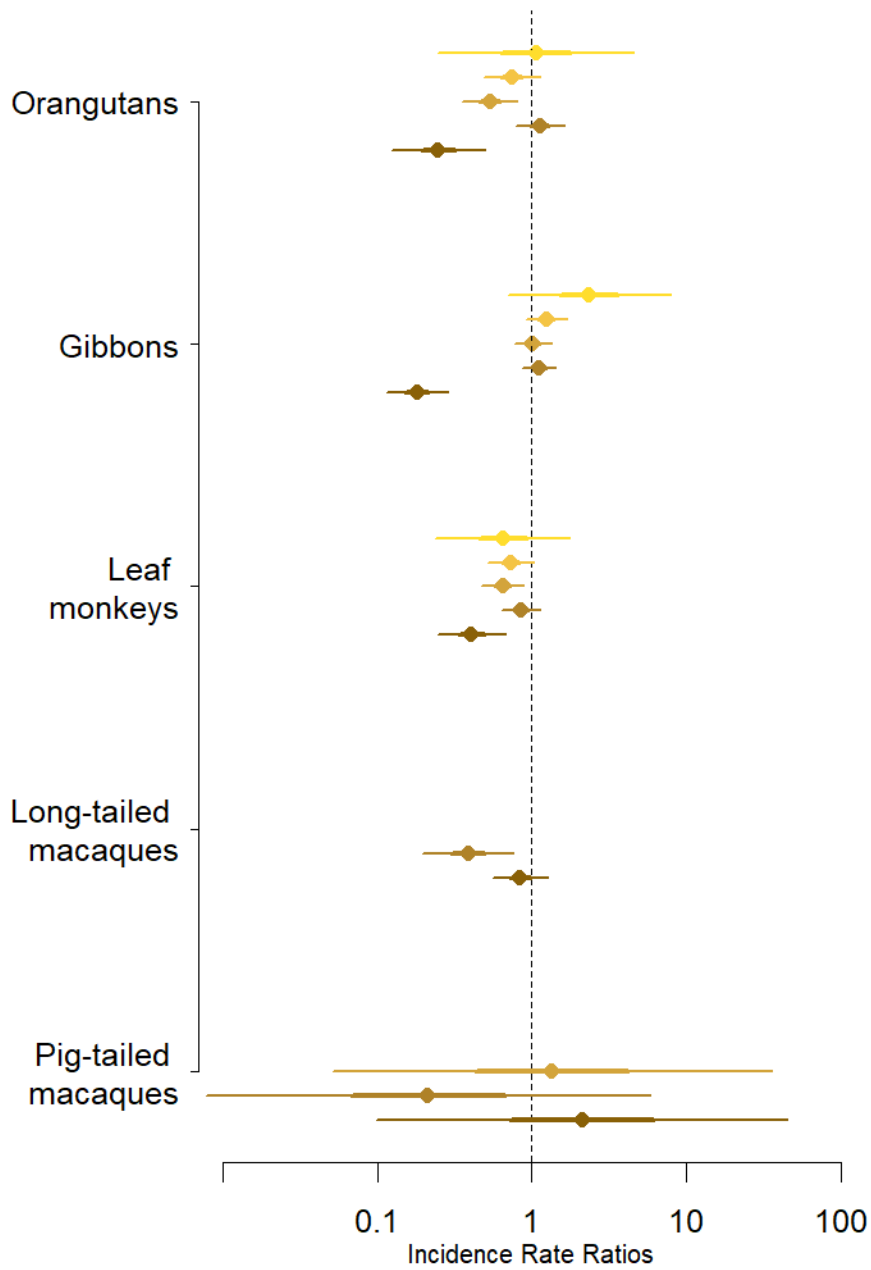
Figure S3.2. Replicate of Figure 3.4 (i.e. matching color scheme and habitat organization where elevations are increasing for each primate's effects), but these effect sizes summarize models that exclude observations in both lowland swamp habitats. Thus, for these models, the lowest elevation habitat is the Alluvial bench.

Chapter 4: Bornean Primate Range Shifts Are Not Fully Explained by Local Trends in Food Availability or Climate

4.1 Abstract

Climate change is often singled out as a driver of extant species' range shifts, but quantitative evidence that empirically links climate to such shifts is surprisingly limited. Additionally, our knowledge of range shifts is largely based on models that do not consider the role of abiotic effects in the context of species' biological environments, and often relies on coarse-grained climate data that may not reflect conditions experienced by populations on local scales. Optimizing models of climate-driven range shifts is critical to predict change and understand how climate may interact with other ecological and anthropogenic processes to determine species' future behavior and distributions. We built generalized linear models to examine whether local trends in temperature, rainfall, and food availability may be driving the ongoing range shifts observed in several sympatric primates (*Pongo pygmaeus, Hylobates albibarbis, Presbytis rubicunda*, *Macaca fascicularis,* and *Macaca nemestrina*) over a 14-year period along an elevational gradient at Gunung Palung National Park in Indonesian Borneo. We found that the influence of ecological predictors was dependent on elevation, but overall neither minimum temperature, cumulative rainfall, nor food availability were consistently reliable predictors of primate abundance trends. Maximum temperature did not strongly impact abundance for any species at any elevation. The most consistent predictor of primate abundance was a linear effect of time, suggesting that prominent ecological drivers of distribution patterns were not included in

our models. Further, while Borneo is on average becoming hotter and drier as climate changes, local conditions at Gunung Palung were primarily getting cooler and wetter. This disparity reinforces knowledge that local weather conditions can differ from regional trends, thus highlighting the importance of empirically measuring local conditions and the role of elevation gradients as climate refugia, provided that they are accessible given species' behavioral limitations on dispersal and geographic boundaries.

4.2 Introduction

For several decades, species range shifts have been observed in many taxa across many kinds of terrestrial environments (Hughes, 2000; Parmesan et al., 1999). These shifts commonly occur along latitudinal or elevational environmental gradients, where species can track changes in their environments as permitted by habitat connectivity (Schloss et al., 2012). Climate change is often highlighted as a primary catalyst of range shifts, most often warming temperatures (e.g. Chen et al., 2011; Moritz et al., 2008) but sometimes changing precipitation regimes are implicated as well (Mccain & Colwell, 2011; Tingley et al., 2012). Such associations are consistent with longstanding ecological theory that climate drives species distributions (Grinnell, 1917; MacArthur 1972) and, more recently, that the speed of contemporary climate change may exceed a population's ability to adapt in-place (Phillimore et al., 2010). Describing the nature of species-climate relationships is essential because it informs our understanding of both climate's role in species' evolutionary pasts and informs predictions about how future climate changes will affect extant populations.

There are, however, several key factors that limit our ability to attribute contemporary climate change as an underlying cause of range shifts (Parmesan et al., 2011). First, in most

empirical studies, climate is only identified as an apparent driver of change. In these cases, a direct link between shifts and changing climate conditions is assumed rather than empirically demonstrated (e.g. Peñuelas & Boada, 2003). These links are critical to establish because they are key to the premise of climate-driven turnovers in the "favorability" of habitat conditions, such as predictions that tropical upland forests will increase in quality relative to tropical lowland forests (Struebig et al., 2015).

Secondly, the considerable emphasis on increasing temperature as an apparent cause of change largely omits the role of dynamic biological factors such as food availability (Potts et al., 2020), food quality (Rothman et al., 2015), forest structure (Deb et al., 2018), and other interactions among species (Post, 2013). Indeed, vegetation is known to mediate the effects of climate on biodiversity (Kay et al., 1997), and biotic factors can stress species at both individual and population levels (Kamilar & Beaudrot, 2018). Thus, in some cases, range shifts may be more proximately linked to biotic changes than abiotic changes directly. Together, both biotic and abiotic links to climate are critical to understanding complex cascading community effects as different species respond to different factors at different rates (Pecl et al., 2017). Additionally, the impact of specific abiotic and biotic factors may vary across a population's range, especially if a population inhabits a range of habitat conditions. For example, orangutan density along an elevational gradient at Gunung Palung National Park was closely related to food availability in lowland forests, while temperature and rainfall only impacted orangutans' abundance at high elevations (Marshall et al., 2021).

Finally, distribution studies often rely on coarse-resolution climate data from regional weather stations or values extrapolated from remote sensing rather than empirical measurements of local conditions. Analyzing local climatic conditions is particularly crucial at smaller scales,

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where macroclimate data may overestimate the likelihood of range shifts. There is considerable heterogeneity in microclimates at high-resolution spatial scales, and variability in local ground-level conditions often exceeds the magnitude of large-scale climate changes projected over the next century (Maclean & Early, 2023).

Collectively, these shortcomings may be even more impactful in the tropics, where biodiversity is the highest and biotic interactions thus more impactful (though less understood than in temperate latitudes: Beaudrot et al., 2019). Tropical endotherms especially may be disproportionately impacted by warming temperatures because they are likely adapted to a relatively narrow range of temperatures that may be exceeded within the century (Khaliq et al., 2014). Further, range shifts in the tropics are most likely to occur along elevational gradients where novel conditions can be reached without traversing long distances and dispersal is generally less restricted (Burrows et al., 2011). In general, range shifts along elevational gradients are more variable and less predictable compared with latitudinal shifts, suggesting a particularly complex mix of mechanisms is at play (Neate-Clegg & Tingley, 2023). The substantial habitat heterogeneity along these gradients also reinforces the significance of microclimates and increases the possibility that there are pronounced differences between actual local conditions and those extrapolated from coarse-resolution data.

In the tropics, there is relatively scant empirical evidence to support widespread predictions of climate-induced range shifts, especially in long-lived species (Beaudrot et al., 2018; Bernard & Marshall, 2020) that require longer time series data to distinguish between true range shifts and short-term movements (Lenoir & Svenning, 2013). One of the few such cases was documented in several primate species at the Cabang Panti Research Station (CPRS) in Gunung Palung National Park, Indonesian Borneo. At this site, along an unfragmented, 5 – 1100

m.a.s.l. elevational gradient, a previous study analyzed 35 years of primate distribution records and found that four of the five commonly-observed primates (Bornean orangutans [*Pongo pygmaeus wurmbii*], Bornean white-bearded gibbons [*Hylobates albibarbis*], red leaf monkeys [*Presbytis rubicunda*], long-tailed macaques [*Macaca fascicularis*]) were disproportionately declining in abundance in the lowland forests relative to upland forests (Chapter 3, this dissertation). Gibbons and orangutans also experienced relative abundance increases in the upland forests. Together, these patterns are consistent with the expectations of two classes of range shifts, rear-edge range retractions and front-edge upward leans (Lenoir & Svenning, 2013; Lenoir & Svenning, 2015).

Here, we further investigate these primate distribution dynamics and seek to clarify their potential abiotic and biotic drivers. Specifically, we tested for associations between primate abundance, maximum temperature, minimum temperature, cumulative rainfall, and food availability, all of which were monitored along with primate abundance at CPRS between 2007-2020. Importantly, our results will also assess the consistency between local heterogeneous weather conditions and regional Bornean climatic trends, the latter of which are generally trending hotter and drier over time (Kumagai et al., 2013; Munawar et al., 2022).

4.3 Methods

4.3.1 Study Site

We conducted field research at the Cabang Panti Research Station (CPRS) at Gunung Palung National Park, Indonesian Borneo (1°13'S, 110°7'E). CPRS is characterized by an elevational gradient ranging from 5 - 1100 m.a.s.l. comprising two ridges separated by an east to west-running river valley. There are seven distinct forest types that differ in elevation, geology,

soil type, forest structure, and species composition (see Marshall et al., 2021). Forest types

include the peat swamp, freshwater swamp, alluvial bench, and lowland sandstone in the

Table 4.1 Total distances sampled (km) from 2007-2020 by forest type and elevational zone.

Zone	Habitat	Elevation range (median elevation), m.a.s.l.	Kilometers walked
Upland	Montane	750-1100 (925)	1795.1
	Upland Granite	350-800 (575)	3116.6
Midland	Lowland Granite	200-400 (300)	2018.2
Lowland	Lowland Sandstone	20-200 (110)	1629.7
	Alluvial Bench	5-50 (27.5)	1653.9
	Freshwater Swamp	5-10 (7.5)	1323.8
	Peat Swamp	5-10 (7.5)	2196.0

lowlands, lowland granite forests in the mid-elevation range, and upland granite and montane forests at higher elevations (Table 4.1; Cannon et al., 2007; Marshall et al., 2014). Due to CPRS's proximity to the coast, elevational zones are compressed (the Massenerhebung Effect: Grubb, 1977), resulting in substantial habitat differences over short spatial distances and the presence of true montane forests above 750 m.a.s.l. (Cannon et al., 2007).

4.3.2 Data Collection

4.3.2.1 Primate abundance

We assessed primate abundance using systematic vertebrate censuses (Marshall, 2004; Marshall et al., 2014) from September 2007 through September 2020. During this time, fourteen census routes (mean length 3.4 ± 0.24 km) that follow established trails were walked twice per month, totaling 13733 kilometers of transect sampled (Table 4.1). Because some censuses routes crossed multiple habitat types, we separated each transect into "segments" by forest type to attribute primate observations to their corresponding habitats. Censuses began at 5:30am at the opposite starting end from the previous sample (of that route) to avoid potential biases in encounter rates associated with primate activity patterns (Marshall, 2004). Observers maintained a consistent walking pace of 0.75-1 km/hr, and censuses took on average 5-6 hours to complete.

Observers recorded the species and group size (and their confidence in the observed group size) of all primates encountered on censuses (Table 4.2). Consistent with analyses in Chapter 3, we only analyzed data where group counts were complete, and excluded carried infants from the analysis. While all recorded observations were visual, primates could be initially detected either by sight or sound; if observers heard a noise that may have come from a primate, they temporarily left the transect to visually confirm if primates were present.

While we designed census routes to sample all forest types as uniformly as possible, we note that two censuses in the montane forest were walked less frequently than the others due to their remoteness and other logistical constraints. While three other censuses included segments in the montane forest (thus the forest type itself was monitored continuously throughout the study period), sampling on those two particular routes occurred only between 2007-2011 and 2019-2020. During the latter period, effort was increased from two to three replicates per census per month to account for the low population density of resident primates. We accounted for differences in sampling over time by including effort (measured in kilometers walked) as an offset term in our generalized linear models.

4.3.2.2 Weather data

We recorded weather data (maximum temperature, minimum temperature, and cumulative rainfall) across twelve weather stations along the elevational gradient. Each weather station consisted of a Taylor analog dual-reading min-max thermometer and a Forestry Suppliers rain gauge with overflow capacity (Marshall et al., 2021). Weather units were carefully placed and monitored to make sure that thermometers did not receive direct sun exposure and rain gauges were uninhibited by overhanging vegetation. Temperature and rainfall data from the station at the field site's camp in the alluvial bench were measured daily, while all other stations were monitored every ten days.

4.3.2.3 Phenology Plots

We monitored plant phenology across 10 randomly placed plots in each of the seven forest types (70 plots total). Each plot was 0.1 or 0.2 ha in size, and a total of 1.5 ha of plots were monitored per month per forest type. As with primate censuses, the montane forest was sampled

Table 4.2. The total number of groups and independently traveling individuals (i.e. excluding carried infants) encountered, average group size ± SD per primate species per habitat. Tallies only include encounters for which complete group sizes were recorded. Habitats are ordered by ascending elevation. No long-tailed macaques were observed in the upland elevational zone.

Primate	Zone	Habitat	Total group encounters	Total number of individuals	Mean number of independent travelers per group ± SD
Orangutans	Upland	Montane	13	19	1.5 ± 1.0
		Upland Granite	74	93	1.3 ± 0.5
	Midland	Lowland Granite	54	75	1.4 ± 0.5
	Lowland	Lowland Sandstone	80	114	1.4 ± 0.6
		Alluvial Bench	90	131	1.5 ± 0.7
		Freshwater Swamp	53	77	1.5 ± 0.6
		Peat Swamp	190	275	1.5 ± 0.6
Gibbons	Upland	Montane	42	71	1.7 ± 0.8
		Upland Granite	325	675	2.1 ± 1.0
	Midland	Lowland Granite	308	639	2.1 ± 1.1
	Lowland	Lowland Sandstone	337	840	2.5 ± 1.3
		Alluvial Bench	208	516	2.5 ± 1.3
		Freshwater Swamp	140	290	2.1 ± 1.1
		Peat Swamp	223	534	2.4 ± 1.2
Leaf Monkeys	Upland	Montane	48	114	2.4 ± 1.2
		Upland Granite	301	879	2.9 ± 1.5
	Midland	Lowland Granite	253	832	3.3 ± 1.9
	Lowland	Lowland Sandstone	272	863	3.2 ± 1.7
		Alluvial Bench	288	1018	3.5 ± 2.0
		Freshwater Swamp	140	463	3.3 ± 1.9
		Peat Swamp	126	359	2.9 ± 1.5
Long-tailed Macaques	Upland	Montane	NA	NA	NA
		Upland Granite	NA	NA	NA

	Midland	Lowland Granite	2	2	1.0 ± 0.0
	Lowland	Lowland Sandstone	48	306	6.4 ± 4.5
		Alluvial Bench	234	1343	5.7 ± 3.5
		Freshwater Swamp	108	627	5.8 ± 3.4
		Peat Swamp	9	46	5.1 ± 4.3
Pig-tailed Macaques	Upland	Montane	2	5	2.5 ± 2.1
		Upland Granite	2	7	3.5 ± 2.1
	Midland	Lowland Granite	14	67	4.8 ± 3.3
	Lowland	Lowland Sandstone	12	31	2.6 ± 2.1
		Alluvial Bench	6	17	2.8 ± 2.3
		Freshwater Swamp	13	53	4.1 ± 4.2
		Peat Swamp	18	70	3.9 ± 3.4

less frequently than other habitat types, with the ten montane phenology plots only monitored from 2007-2011 and 2019-2020. Stem counts varied considerably among forest types but averaged 115 ± 45 monitored stems per plot.

In each monthly plot visit, every tree and liana that met a certain DBH size threshold (at least 14.5 cm for trees, and 3.5 cm for lianas), as well as every hemi-epiphytic fig whose roots reached the ground, were visually assessed for reproductive status. These DBH thresholds were

determined by the size most plants were likely to reach reproductive maturity (Marshall et al., 2021). Reproductive state for each monitored stem was recorded as one of six statuses: reproductively inactive, bearing flower buds, bearing immature fruit, bearing mature fruit, or bearing ripe fruit (Cannon et al., 2007).

To quantify food availability, we calculated the total number of stems per hectare that bore mature or ripe fruits for each 30-day sampling period. We separated mature from ripe fruits to account for the fact that primates at CPRS have different dietary preferences: for example, highly frugivorous gibbons feed almost exclusively on ripe fruits, while leaf monkeys feed on unripe mature fruits far more frequently (Marshall, 2004). We also analyzed figs as a separate food category given that they do not follow the phenological patterns of most other fruiting taxa at CPRS. Specifically, figs fruit with a uniquely high degree of asynchrony across their range at CPRS and are thus consistently available during low fruiting periods as fallback foods (especially for gibbons: (Dillis et al., 2015; Marshall, 2009)).

We do acknowledge, however, that our measures of food availability are coarse, and likely include fruits that primates do not habitually eat. We chose not to attempt to correct for this by only including specific fruiting taxa because food preferences almost certainly change across the elevation gradient (Owens et al., 2015), and our knowledge of primate feeding behavior at CPRS is biased towards lower elevations where primates are observed more frequently. We also note that our analysis does not account for crop size, which likely varies both among fruiting taxa and within a given taxon over space.

4.3.3 Analyses

We built species-specific generalized linear models to quantify the effects of temperature, precipitation, and food availability on primate counts. We analyzed time as a linear variable by

grouping observations into standardized 30-day sampling blocks (n = 158 blocks), which are represented in our models as continuous integers. Count data were overdispersed, thus all models were built on a negative binomial distribution using the function "glm" in the "stats" package in R (R version 4.2.2, R Core Team, 2022).

The previous study that described distribution dynamics over time at CPRS used habitat type as a proxy for elevation (this dissertation, Chapter 3). Here, we elected to group the seven habitats into three distinct elevation "zones" (Table 4.2): a lowland zone ranging from 5 to 200 m.a.s.l. (incorporating the peat swamp, freshwater swamp, alluvial bench, and lowland sandstone habitats), a midland zone from 200 to 400 m.a.s.l. (the lowland granite habitat), and an upland zone ranging from 400 to 1100 m.a.s.l. (the upland granite and montane habitats). There is a precedent for binning elevational gradients in similar ways to describe distribution dynamics of long-lived species over time (e.g. Beaudrot et al., 2019), but there are also justifications for this strategy that are intrinsic to the CPRS system. The first reason is methodological: our metrics of weather and food availability are habitat-specific with widespread, but not unilateral, consistency. Weather stations were installed systematically with respect to elevation, rather than habitat type, and while some habitats contain multiple stations (e.g. n = 7 stations between the upland granite and montane habitats), others do not contain any (n = 0 in the peat swamp and lowland sandstone forest types). Additionally, as previously noted, phenology was not measured in montane forests between 2012-2019. The second reason is biological: although many primates at CPRS are dispersal restricted due to small home range sizes, some individual group territories cross multiple habitat types. Thus, grouping predictor variables by zone may more accurately represent the full range of conditions primates are exposed to rather than maintaining individual habitat distinctions.

To assess the relative impacts of biotic and abiotic predictors on primate abundance, we built a "global" model for each primate species that incorporates all predictor terms. No predictor variables were sufficiently correlated (i.e. a correlation coefficient > 0.6) to warrant concerns about collinearity. Further, each continuous predictor is centered and standardized on the mean of their respective distributions to permit direct comparisons of their effect sizes (Gelman, 2008). We also modeled interaction effects between each continuous predictor and zone. An interaction term between zone and time acknowledges that trends in primate abundances of primates are contingent on elevation (this dissertation, Chapter 3). Similarly, interaction terms between other predictors and zone accounts for the likelihood that the impacts of weather and food availability are not homogeneous along the elevational gradient (Marshall et al., 2021). The effects of predictors were considered reliable when the 95% confidence intervals around their maximum likelihood estimates did not overlap zero (or, on an odds ratio scale, odds of one).

4.4 Results

4.4.1 Trends in primate abundance over time

Over 157 consecutive months (which converts to 158 30-day sampling periods), census observers encountered and counted all independently traveling individuals in 554 groups of orangutans (n = 784 independently traveling individuals), 1583 groups of gibbons (n = 3565 individuals), 1428 groups of leaf monkeys (n = 4528 individuals), 401 groups of long-tailed macaques (n = 2324 individuals), and 67 groups of pig-tailed macaques (n = 250 individuals) (Table 4.2). During this time, primate distribution patterns were largely consistent with previous long-term findings from CPRS (this dissertation, Chapter 3). Specifically, abundance declined for all focal species except pig-tailed macaques, with counts in the lowland forests decreasing

more rapidly relative to upland forests for orangutans, gibbons, and leaf monkeys (Table 4.3, Fig. 4.1). Relative abundance increases were the most positive for pig-tailed macaques in the mid-elevation zone (increased odds of 2.11 ± 0.97 per standardized unit increase in time), followed by orangutans in the uplands (1.96 ± 0.23), gibbons in the mid-elevation zone (1.89 ± 0.15) and gibbons and leaf monkeys in the uplands (1.89 ± 0.15 and 1.16 ± 0.15, respectively). These odds were consistent between models whether or not additional abiotic and biotic predictors were included (Table 4.3, Fig. 4.2).

4.4.2 Relative influence of weather and food availability on primate distributions

There were only a small number of cases where weather or food availability reliably impacted primate counts (i.e. confidence intervals do not overlap one) within certain elevation zones (n = 1 case between a weather predictor and primate counts within a zone, n = 3 cases between food availability and zone-specific primate counts). Similarly, there was little consistency in the effects of a single predictor for any given primate species over space. Across predictors, however, the strongest relationships between weather or food availability and primate abundance were in the low- and mid-elevation zones.

The sole case of a completely reliable weather predictor (i.e. confidence intervals around beta coefficients did not overlap zero) for any primate was with rain in the lowland forests, where the odds of counting long-tailed macaques decreased by 0.71 (± 0.13 SE) per each standardized unit increase in cumulative rainfall (Table 4.4, Fig. 4.3). Minimum temperature was also a relatively strong predictor of orangutan counts in the lowland (1.27 ± 0.14) and upland (2.80 ± 0.60) elevation zones, but not in the mid-elevation zone where minimum temperatures are highest (minimum temperature mean = 21.34 ± 0.61 SD; Table 4.4).

Within-zone food availability was a stronger and more consistent predictor of orangutan counts than for any other primate. The odds of counting orangutans were strongly related to standardized unit increases in fruiting mature stems per hectare in the lowlands (1.43 ± 0.13) and fruiting ripe stems in the midlands (2.21 ± 0.36). Several metrics of food availability in the uplands also positively impacted orangutan counts in that zone, however the relationships were weaker than in lower elevation forest types (increased odds based on number of ripe stems [1.42 ± 0.27] and number of ripe figs [1.53 ± 0.26]). There were weaker influences of one or more food metrics on the abundance of other primates, but only in lowland or midland zones (increased odds of 1.29 ± 0.16 for gibbons in the midlands as mature stems increased; increased odds of 1.17 ± 0.10 for leaf monkeys in the lowlands as mature figs increased; increased odds of 2.35 ± 0.49 and 1.80 ± 0.45 per unit increase in ripe and mature stems, respectively, for pig-tailed macaques in the lowlands). Ripe figs also had a reliably negative impact on long-tailed macaques in the lowlands, with the odds of counting individuals decreasing by 0.70 (± 0.180) per standardized unit increase in the number of ripe figs fruiting.

4.4.3 Spatiotemporal trends in weather and food availability across elevation zones

Patterns in temperature and precipitation at CPRS varied across the elevational gradient, but collectively, they were inconsistent with the near-unilateral warming trends described across primate ranges both globally and regionally (Graham et al., 2016; Munawar et al., 2022). At CPRS, only maximum temperature in the mid-elevation forests increased over time (0.002 ± 0.001 SD), while maximum temperatures decreased in both the lowland (-0.002 ± 0.001 SD) and upland (-0.005 ± 0.001 SD) forests by an estimated 0.31 and 0.81 °C between 2007 and 2020,

Table 4.3. Back-transformed (exponentiated) beta coefficients and standard errors for the effect of time on primate counts, with and without additional abiotic and biotic predictors. While there were a small number of encounters with long-tailed macaques in midland forests and pig-tailed macaques in midland and upland forests (see Table 4.2), these observations were excluded from analyses because the small sample size prevented model convergence.

Primate	Zone	Beta coefficient (odds scale) of time with other predictors in the model	Beta coefficient (odds scale) of time without other predictors in the model
Orangutans	Uplands	2.31 ± 0.31	1.96 ± 0.23
	Midlands	0.83 ± 0.34	0.77 ± 0.30
	Lowlands	0.57 ± 0.13	0.59 ± 0.10
Gibbons	Uplands	1.38 ± 0.17	1.30 ± 0.13
	Midlands	1.84 ± 0.17	1.89 ± 0.15
	Lowlands	0.52 ± 0.09	0.52 ± 0.07
Leaf monkeys	Uplands	1.17 ± 0.20	1.16 ± 0.15
	Midlands	0.72 ± 0.21	0.80 ± 0.18
	Lowlands	0.87 ± 0.11	0.83 ± 0.08
Long-tailed macaques	Uplands	NA	NA
	Midlands	NA	NA
	Lowlands	0.64 ± 0.16	0.76 ± 0.13
Pig-tailed macaques	Uplands	NA	NA
	Midlands	2.11 ± 0.97	2.00 ± 0.89
	Lowlands	1.08 ± 0.55	1.02 ± 0.46

Table 4.4. Descriptive statistics and basic linear model outputs for changes over time in all abiotic and biotic predictors (these relationships are plotted in Figure 3). For each predictor (columns), we report median values ± standard deviation over the complete time series, beta coefficients ± standard errors (rounded to three decimal places) describing unit changes in predictor values over each 30-day sampling period, and the calculated change in each predictor over the 14-year study period. For example, an estimated 0.214 mm increase in cumulative rainfall in the lowland forests over 158 sampling periods equals a 33.85mm increase in rainfall per sampling period in 2020 relative to 2007).

	Zone	Rain	Min temp	Max temp	Mature stems (all)	Ripe stems (all)	Mature figs	Ripe figs
Units		(mm per 30-day period)	°C	°C	Stems per hectare	Stems per hectare	Stems per hectare	Stems per hectare
Median ± SD	Uplands	311.85 ± 159.09	19.27 ± 0.49	27.24 ± 0.84	23.29 ± 12.49	9.88 ± 5.98	0.10 ± 0.24	0.04 ± 0.17
	Midlands	290.44 ± 158.57	21.34 ± 0.61	28.88 ± 0.70	16.19 ± 12.79	4.66 ± 3.89	0.15 ± 0.30	0.09 ± 0.26
	Lowlands	348.37 ± 175.02	20.79 ± 0.88	28.13 ± 0.68	21.30 ± 10.62	6.49 ± 4.06	0.29 ± 0.24	0.13 ± 0.16
Beta coefficient ± SE	Uplands	-0.02 ± 0.28	-0.001 ± 0.001	-0.005 ± 0.001	0.06 ± 0.02	-0.07 ± 0.01	0.001 ± <0.000	<0.000 ± <0.000
	Midlands	0.22 ± 0.27	-0.001 ± 0.001	0.002 ± 0.001	0.05 ± 0.02	-0.02 ± 0.01	<0.000 ± 0.001	-0.001 ± <0.000
	Lowlands	0.21 ± 0.30	-0.005 ± 0.001	-0.002 ± 0.001	0.06 ± 0.02	-0.03 ± 0.01	<0.000 ± <0.000	0.001 ± <0.000
Total estimated increase or decrease over duration of study period	Uplands	-3.17	-0.19	-0.81	9.80	-11.04	0.10	0.03
	Midlands	34.86	-0.15	0.37	8.39	-2.87	0.07	-0.08
	Lowlands	33.85	-0.77	-0.31	9.57	-5.02	-0.04	-0.18

respectively (Table 4.4, Fig. 4.3). Minimum temperatures dropped but were relatively stable in the mid-and upland elevation zones, with respective declines of 0.15 and 0.19 °C

through the study period, while minimum temperatures dropped more drastically in the lowland forests by an estimated 0.77 °C.

Interestingly, understory temperatures at CPRS did not strictly decline with elevation. While the upland forests were coolest, as expected (mean minimum temperature = 19.27 ± 0.49 °C; mean maximum temperature = 27.24 ± 0.84 °C), average minimum and maximum temperatures were slightly higher in the mid-elevation zone (21.34 ± 0.61 and 28.88 ± 0.70 °C, respectively) than the low-elevation zone (20.79 ± 0.88 °C and 28.13 ± 0.68 °C) (Table 4.4, Fig. 4.4). This suggests that declines in temperature with increasing elevation are not universal and complicates the standard application of tropical elevation gradients as natural laboratories with predictable temperature controls (Malhi et al., 2010).

Precipitation trends at CPRS also varied along the elevational gradient. Monthly cumulative rainfall remained stable in the uplands (rainfall decreased only by an estimated 0.02 ± 0.28 mm per month) while modeled rainfall totals in the lowland and midland forests were 33.85 mm and 34.86 mm higher, respectively, in 2020 than they were in 2007 (Table 4.4, Fig. 4.3). Thus, CPRS is getting wetter over time while regionally, the Bornean climate is getting drier (Kumagai et al., 2013; Yatagai et al., 2012). At face value, the inconsistency between local and regional conditions is less surprising than the lack of parity between local and regional temperature patterns because, on a global scale, climate-driven precipitation changes are projected to be much more localized (Graham et al., 2016). Still, our findings emphasize the value of measuring local weather conditions when making biological inferences on fine-grained scales (Maclean & Early, 2023).

Secular trends in primates' biotic environments were evident across all metrics of food availability included in our analyses. In particular, there were sharp declines in the number of stems per hectare with ripe fruit per hectare in all elevational zones (declines of 0.03 ± 0.01 stems in lowland forests, 0.02 ± 0.01 stems in midland forests, and 0.07 ± 0.01 stems in upland forests per 30-day sampling period) and corresponding increases in the number of stems per hectare with mature fruit (increases of 0.06 ± 0.02 stems in lowland forests, 0.05 ± 0.02 stems in midland forests, and 0.06 ± 0.02 stems in upland forests per 30-day sampling period) (Table 4.4, Fig. 4.3). When figs were isolated, trends in their fruiting patterns were not as drastic, however there were discernible declines in ripe fig availability in the lowland forest. Specifically, there were an estimated 0.18 fewer figs with ripe fruit per hectare in 2020 than in 2007, a decline that surpasses the mean lowland density of ripe figs per hectare (0.13 ± 0.16) over the duration of the study period.
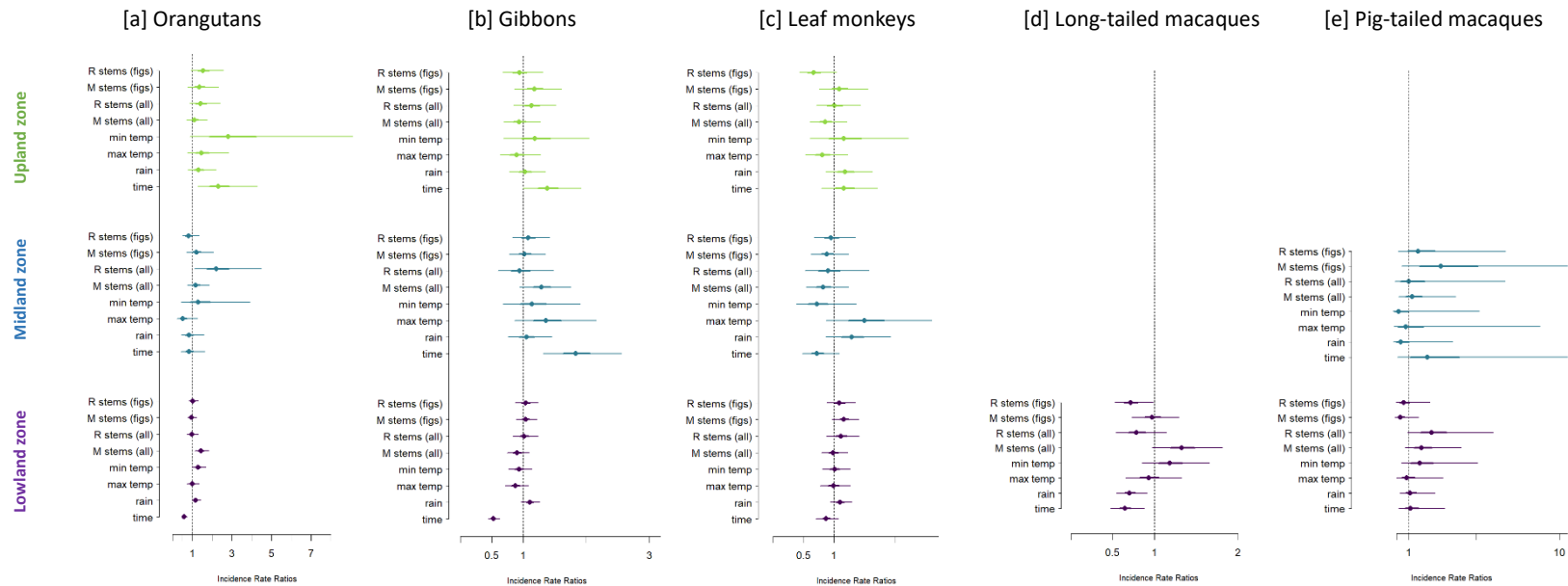
Figure 4.1. Back-transformed (exponentiated) beta coefficients for primate-specific models indicating the odds of counting individuals as influenced by zone-specific effects of time, rainfall, maximum temperature, minimum temperature, the number of stems with mature fruit per hectare, the number of stems with ripe fruit per hectare, the number of stems with mature figs per hectare, and the number of stems with ripe figs per hectare. Points to the left of the dotted line at an odds ratio = 1 indicate decreasing odds of counts as time increases, i.e. a negative effect of time. Lines represent 95% (thin) and 50% (thick) confidence intervals around the maximum likelihood estimate for each effect. Beta coefficients for time correspond to column "Beta coefficient (odds scale) of time with other predictors in the model" in Table 4.3. Note that the x-axis scale differs among panels.
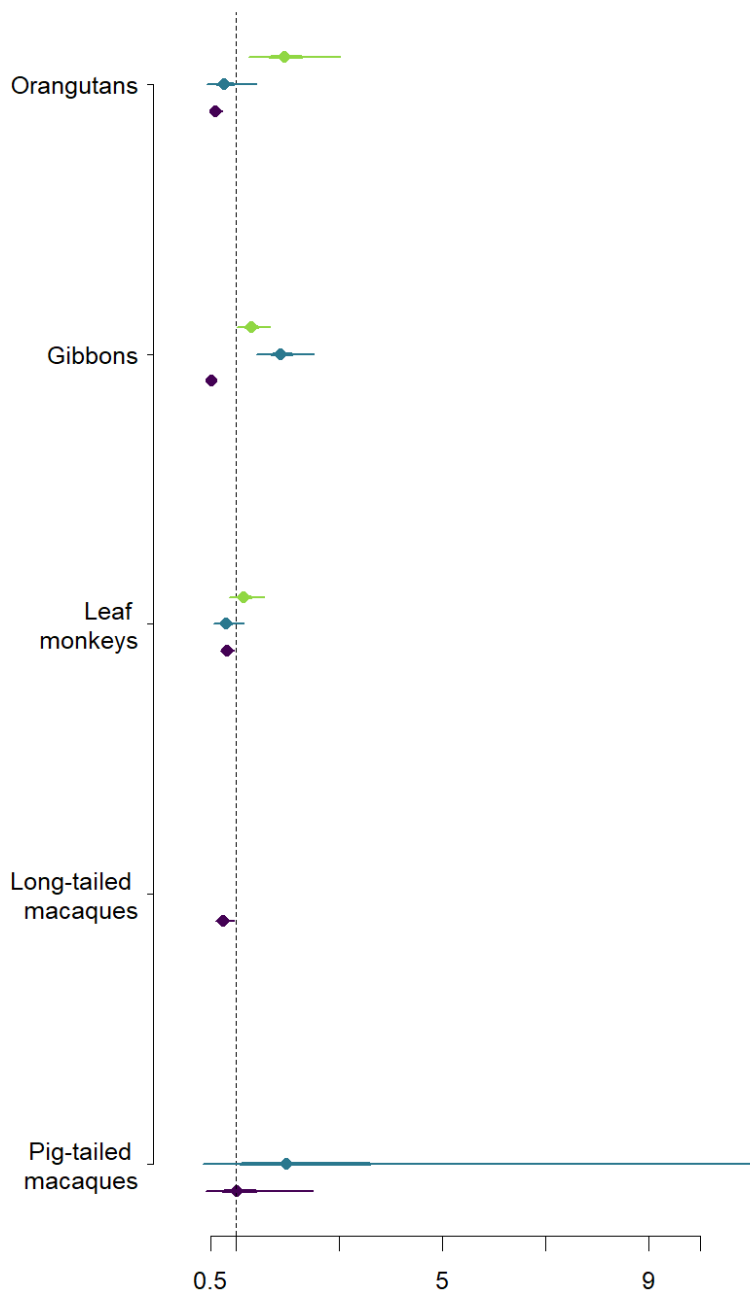
Figure 4.2. Back-transformed (exponentiated) beta coefficients indicating the odds of counting primates over time with no additional predictors. Colors of zones correspond to Fig. 4.1 and are ordered by increasing elevation (purple = lowland forests, blue = midland forests, green = upland forests). Points to the left of the dotted line at an odds ratio = 1 indicate decreasing odds of counts as time increases, i.e. a negative effect of time. Lines represent 95% (thin) and 50% (thick) confidence intervals around the maximum likelihood estimate for each effect. Beta coefficients correspond to column "Beta coefficient (odds scale) of time without other predictors in the model" in Table 4.3.
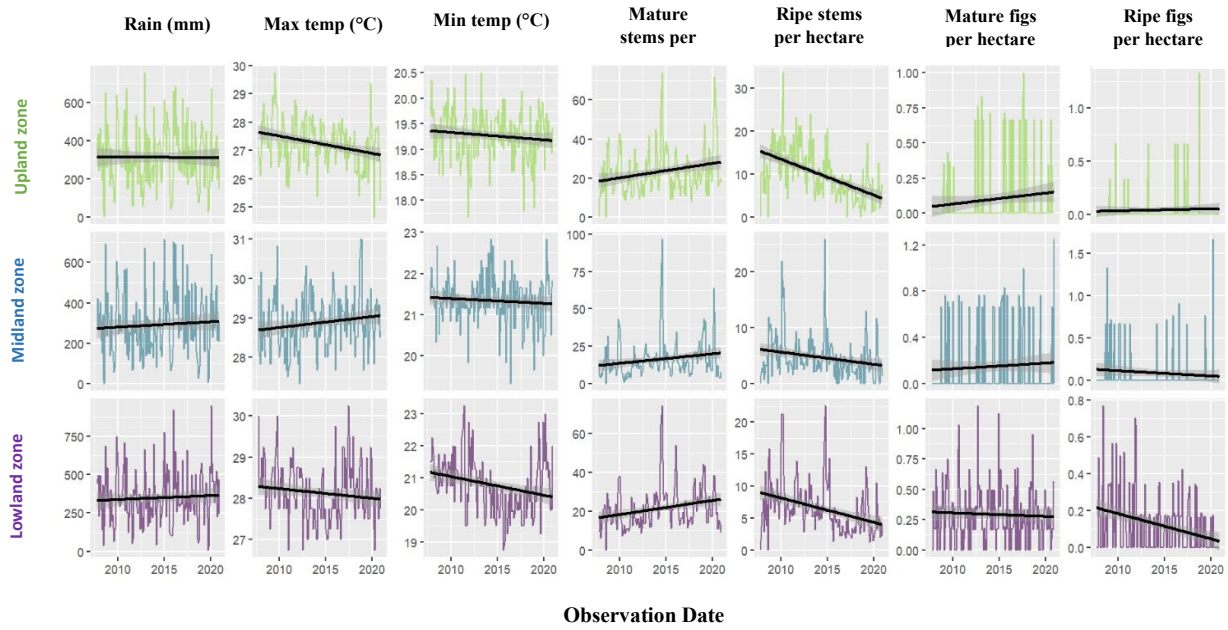
Figure 4.3. Linear regressions for each abiotic and biotic predictor values from 2007-2020 (columns) across the three elevational zones (rows). The y-axes are scaled differently for each panel to make trends through time more visible, and y-axis units for each predictor are indicated in their respective column headings. Beta coefficients from these models are indexed in Table 3.4.
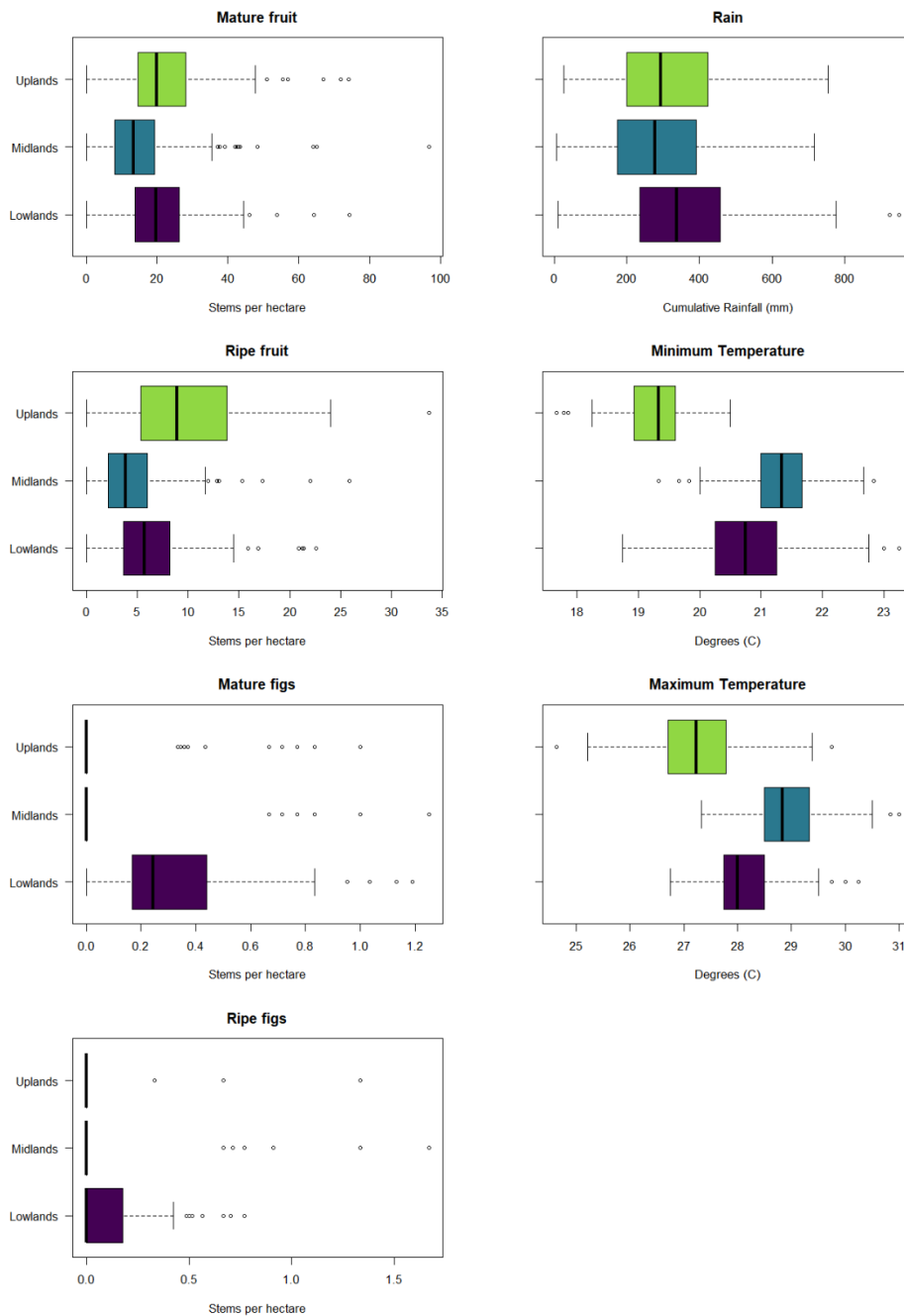
Figure 4.4. The distribution of values for each biotic (left column) and abiotic (right column) predictor in the three elevational zones. Boxplots indicate the middle 50% of observations, and the median value is indicated by the solid black vertical bar. Note that the x-axis of each panel is different to make it easier to compare values among zones for each predictor. Values of zone-specific medians are shown in Table 4.4.

4.5 Discussion

4.5.1 The linear effect of time remains a dominant predictor of abundance

The abiotic and biotic predictors we used in our analyses are known to affect species'

ranging patterns both at CPRS (Marshall et al., 2021) and more broadly (Beaudrot et al., 2019).

Thus, the consistent effects of time across models that do and do not include additional

environmental predictors bolsters findings of a previous analyses that found most primates at

CPRS were in decline, but also showed indicators of upward "leans" in their distributions

(Chapter 3).

These findings have several important implications. First, our results are consistent with

evidence that shifting ranges, even when shifts are feasible (Schloss et al., 2012), may not

prevent population declines (Parmesan, 2006). Secondly, the consistent impact of time indicates

that there are drivers of primate abundance at CPRS that induce distribution patterns consistent

with the expectations of warming temperatures (i.e. disproportionate lowland abundance declines

relative to upland abundance), but which are not accounted for in our models. Such processes

could include habitat loss due to deforestation (Zamzani et al., 2009), forest fires, whether

directly impacting primates through habitat loss or indirectly through the damaging effects of

smoke (Page et al., 2009), hunting (Marshall et al., 2006), and encroachment from invasive

species such as *Bellucia pentamera* (Dillis et al., 2018).

4.5.2 Temperature does not strongly impact trends in primate distributions

One particularly notable trend is the scarce evidence that temperature reliably impacts

primate distribution patterns at CPRS. There were no strong relationships between maximum

temperature and primate counts, and only limited support for the influence of minimum

temperatures. Abundance of just one primate species, orangutans, was found to be positively

associated with minimum temperatures, and only in the lowland and upland elevation zones, where average minimum temperatures are cooler than in the midlands (Fig. 4.4). The reason why temperatures at CPRS do not follow a linear decline as elevation increases is unclear, however it could be due to a stronger insulating effect in the lowland forests because stem densities are higher there relative to the midland zone (Marshall et al., 2014). Biologically, these patterns suggest that minimum temperatures in the mid-elevation zone remain uniquely warm enough such that thermoregulatory capacities of orangutans are not strained.

There are several plausible, non-mutually exclusive explanations for why temperature has only a minor effect on primate abundance at CPRS. First, the direct impact of temperatures on long-term abundance may be limited when other biotic factors (e.g. food availability) are statistically accounted for. This interpretation has widespread implications for the near-ubiquitous assumptions about the effects of increasing temperatures and range shifts (Parmesan, 2006), and reinforces the importance of using caution when projecting range shifts without sufficiently accounting for biological realism (Bahn & McGill, 2013; Pearson & Dawson, 2003). In other studies, direct relationships between temperature and primate occupancy have been less important than biotic metrics such as forest cover (Gregory et al., 2012) or food availability, including in strongly seasonal environments where primates are exposed to greater extremes or regular fluctuations in temperature (e.g. snub-nosed monkeys: Grueter et al., 2012; but see McLester et al., 2019). While many empirical studies have shown that hot temperatures impact primate behavioral and activity patterns, these are usually in more open, hotter, and arid environments (e.g. yellow baboons: Johnson et al., 2015; chimpanzees: Wessling et al., 2018) or in small-bodied, heterothermic primates with higher basal metabolisms (Donati et al., 2011). In comparison, densely-forested environments may better buffer primates from extreme conditions

due to natural insulation provided by forest canopies (De Frenne et al., 2019) and high frequency of microclimates in the understory (e.g. Stuntz et al., 2002).

Concurrently, it is likely maximum temperature changes at CPRS have not reached a threshold where they routinely surpass physiological limitations of medium-large bodied primates in a closed forested environment. Regional weather data indicate that over the last two decades, temperatures are steadily increasing across Borneo (Kumagai et al., 2013; Sukmara et al., 2022), and at accelerated rates of more than 0.4 degrees per decade in West Kalimantan, the province in which CPRS is located (Munawar et al., 2022). In contrast, maximum temperatures at CPRS increased solely in the midland elevation zone by an estimated 0.37 °C over the 14-year study period (Table 4.4, Fig. 4.3). Indeed, the largest magnitude temperature change was an estimated 0.81 °C decrease in maximum temperature in the upland forests, a cooling trajectory that directly contrasts with widespread in situ indicators that the rate of warming increases with elevation (Pepin et al., 2022; Wang et al., 2016). Precipitation patterns at CPRS are also inconsistent with regional climate patterns. While climate across Borneo is on average becoming drier (Kumagai et al., 2013), the low- and mid-elevation forests at CPRS are getting wetter (Table 4.4, Fig. 4.3). Explanations for precisely why weather trends at CPRS diverge from surrounding areas are beyond the scope of this study, but are possibly related to complex interactions between the close proximity of the Gunung Palung massif to the coast, the Australian monsoon system that regulates intra-annual seasonal trends in West Borneo, and El Niño Southern Oscillation cycles that are influential on supra-annual scales (Wich & Van Schaik, 2000). Regardless, the divergent and localized weather trends at CPRS provide further empirical support that elevation gradients may be significant refugia for tropical species if conditions elsewhere become less hospitable.

The lack of strong increasing temperature trends at CPRS could also clarify why temperature was only found to reliably impact orangutans, rather than all primates. Because of their large home ranges, individual orangutans can preferentially track short-term ecological changes across the elevational gradient (Marshall et al., 2021) in a matter distinct from the long-term secular trends in temperature or food availability themselves. For example, in the upland forests, where orangutan counts increase with higher minimum temperatures (Fig. 4.1), modeled orangutan abundance increased over time while minimum temperatures were decreasing (Table 4.4, Fig. 4.3, Fig. 4.5). Other primates, especially gibbons and leaf monkeys, are much more dispersal-restricted due to their smaller home ranges that abut each other closely in space (Marshall, 2004). Thus, individuals of those species are unlikely to disperse in response to short-term changes in environmental conditions. Rather, impacts of temperature would be evident only if secular trends drove a reduction in habitat-specific carrying capacities or if isolated extreme conditions precipitated physiological threshold effects, neither of which have seemingly occurred at CPRS over the duration of the study period.

4.5.3 Dispersal ability mediates the impact of rain and food

In sum, there are a greater number of reliable abiotic and biotic correlates for orangutan abundance than other primates. These species differences, consistent with predictive effects of temperature, are likely a function of the primates' differential dispersal constraints and ability to track short-term spatiotemporal changes in their environment. Specifically, we found that orangutan abundance is positively associated with mature and ripe stems in low- and mid-elevation forests, respectively. These relationships are consistent with previous investigations of orangutan dispersion patterns where food availability positively correlated with orangutan counts in the lowland forests, but not in the uplands (Marshall et al., 2021). Further, Marshall and
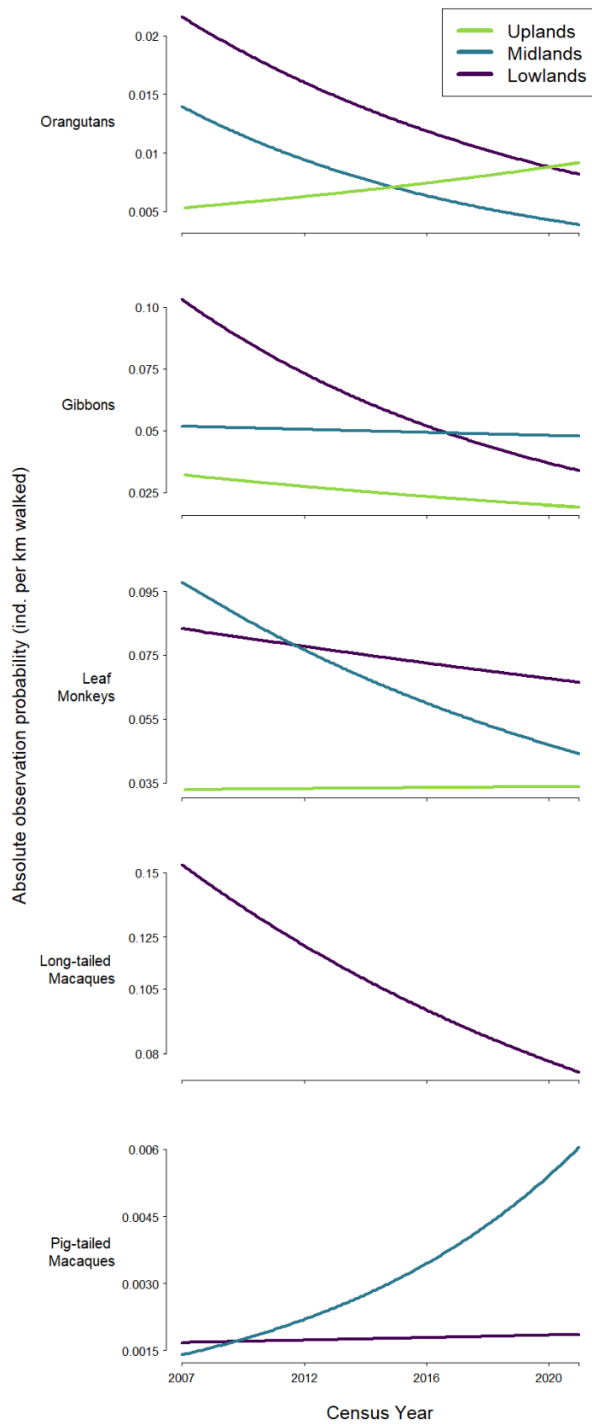
Figure 4.5. Plots of expected primate abundance over time in each elevational zone. Note that the y-axes are scaled differently for each panel. Predictions are based on species-specific models with all abiotic and biotic covariates included, thus these plots hold all predictors other than time at their mean values.

colleagues found that upland orangutan counts were negatively correlated with food abundance in the lowlands, indicating that orangutans use montane forests as a fallback habitat when food in the lowlands is scarce.

Among the primates at CPRS, gibbons have the smallest home ranges (Marshall, 2004) and were not reliably impacted by weather or food availability within any elevational zone. In contrast, long-tailed macaques have home ranges on average 4-5 times larger than gibbons (Lawrence 1989; Marshall, 2004), and long-tailed macaque abundance was negatively associated with both ripe figs and rainfall. A negative association with ripe figs (also observed for leaf monkeys in the upland forest) could indicate a declining capacity to compete with other arboreal vertebrates for a shared food resource. While primates may mitigate competition with other sympatric vertebrates such as hornbills by evolved species-specific preferences for fruit colors and feeding strata (Poulsen et al., 2002), such niche partitioning may dissolve as the number of ripe figs declines (Table 4.4, Fig. 4.3).

Long-tail macaques were the only primate strongly affected by rainfall in our analyses. Because the relationship between rainfall and macaque abundance is negative, in theory, the observed increased rainfall in the lowlands could be driving a reduction in carrying capacity of lowland forests for long-tailed macaques. It is unclear, however, what proximate pathways may link declining primate abundance with rainfall in this system, as other cases where demography varies as a function of rainfall tend to be more common with primates that are strongly seasonal breeders (Campos et al., 2017). For example, reproductive rate of Milne Edward's sifakas declined during years where it rained more (Dunham et al., 2008, 2011), and infant mortality of white-faced capuchins was especially high during periods of intense drought (Campos et al., 2020). In many such cases, precipitation events in either extreme decreased food availability or

quality, which deleteriously impacted the energetic status of female primates and thus their unweaned offspring.

Alternatively, the negative relationship between cumulative rainfall and long-tailed macaque abundance could influence encounter probability more than carrying capacity. Future analyses could test for this possibility by modeling macaque detection probability separately from latent occupancy (MacKenzie et al., 2002). It may be less likely that primates are observed during periods of increased rainfall, especially when ambient temperatures are cooler, as primates reduce activity levels either to shelter from the rain or allocate more energy to thermoregulation (Hanya et al., 2018). Relative to other primates, encounter probability of long-tailed macaques may be disproportionately affected by rainfall due to their high habitat specialization at CPRS (Marshall et al., 2014). Long-tailed macaques are strongly tied to riverine forests, a preference likely due (at least in part) to the thick ground cover and frequent narrow gaps found along riverbanks that is well-suited to long-tailed macaques' locomotor behavior (Cannon & Leighton, 1994; Rodman, 1991). During and following intense periods of rainfall, the primary river at CPRS floods and becomes fast-moving and murky, creating a dangerous environment for macaques that they may avoid by reducing their movement levels.

4.5.4 Alternative explanations for the limited impact of weather and food availability

While we have suggested that observed trends in primate distributions at CPRS are largely driven by ecological factors not included in our analyses, it is also possible that our model structure underrepresents the significance of weather and food availability. We therefore consider three relevant features of our model design, and how future analyses could account for other forms of variation in weather and food availability that may be ecologically relevant for primates.

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One primary consideration is our simplified representation of time. We model time as a linear effect, while the rate of temperature changes in the tropics (and thus the biological impact of these changes) is probably nonlinear (Chavaillaz et al., 2016). Relatedly, we assume that local food availability and weather impact primate abundances in the same period that those environmental variables are measured. While threshold effects driven by extreme conditions may have immediate physiological impact (Welbergen et al., 2008; Zhang et al., 2019), changes to species' distributions are likely to lag behind changes in climate (Alexander et al., 2018; Forero-Medina et al., 2011). Further, the extent of time lags in the tropics is known to vary from days (e.g. rain as an environmental cue of peak fruit periods: Van Schaik et al., 1993) to months (Wiederholt & Post, 2011) to centuries (Fordham et al., 2016); these asynchronous paces among primates and different features of their environment likely create mismatches among interacting species that are difficult to predict (Hobbs et al., 2009; Pecl et al., 2017).

Because we do not account for such complex temporal dynamics, our models may be less likely to reflect expected relationships between certain environmental predictors and primates. For example, availability of figs is known to influence habitat quality for gibbons (Marshall, 2010), but ripe figs were not a reliable predictor of gibbon abundance in the lowlands (Fig. 4.1). While both gibbon abundance and abundance of ripe figs decreased over time in the lowland forest (Fig. 4.3, Fig. 4.5), a statistical relationship between the two may not be apparent in our model if decreases in gibbon abundance lag behind decreases in fig productivity. Future analyses may account for the variable time lag effects by using a moving window approach (van de Pol et al., 2016) or modeling nonlinear effects of time within generalized additive models (Bender et al., 2018).

Secondly, even though the diets of diurnal primates at CPRS largely overlap (Marshall et al., 2009), our models may underestimate the impact of food availability by using the general measure of fruiting stems per hectare. On one hand, our separation of mature and ripe fruits accounts for broad species-specific preferences in preferred diets, and we distinguish figs as a key (gibbon) fallback food. However, we also likely incorporate some fruits primates do not eat (Marshall et al., 2021) and do not isolate other fruiting genera that may be disproportionately significant for primates in certain forest types. It would be difficult to identify these genera without bias: feeding records are primarily collected in lowland forests, where taxa-specific preferences are likely unique from those in upland forests where feeding records are minimal (Marshall 2009; Marshall et al., 2021). Such differences are driven in part by elevational variation in floristic behavior within a given fruit taxon, such as with crop sizes and nutritional value, that our analyses also assume are constant.

Furthermore, although grouping forest types together into elevational zones may be prudent to represent the range of environmental conditions that impact primate occupancy, such binning may mask influential floristic differences among adjacent habitats. In particular, while the peat swamp and montane habitats are binned with other lowland and upland forest types, respectively, the peat swamp and montane forests may be demographic sinks for many vertebrates (Marshall, 2009; 2018) and do not contain fruiting taxa that follow the typical supra-annual masting patterns of taxa in other habitats (Ashton et al., 1988; Cannon et al., 2007). In these low-quality habitats, vertebrate abundance may be less related to within-habitat food availability as it is related to food in other habitats; this stipulation applies in particular to orangutans at CPRS, for which abundance in the montane forest correlates most directly with decreased food availability in non-peat lowland forests (Marshall et al., 2021).

Finally, our weather metrics, especially our measure of cumulative rainfall over a 30-day period, may not capture the influence of extreme weather conditions that are becoming more frequent and severe (Stott, 2016) and may be more impactful for tropical species than changes in average conditions alone (Butt et al., 2015; Harris et al., 2018; Maxwell et al., 2019; Zhang et al., 2019). Extremely hot conditions may surpass mammalian physiological thresholds with immediate effects on behavior (Campos & Fedigan, 2009) and mortality (Welbergen et al., 2008). Similarly, with precipitation, as previously discussed (see discussion section 4.3) many instances where rainfall impacts primate demography are cases of severely wet (e.g. cyclones: Dunham et al., 2011; Pavelka et al., 2003) or arid (intense drought: Campos et al., 2020; Gould et al., 1999) conditions. Future analyses could address the impact of extreme conditions by isolating more specific features of weather patterns over time (e.g. modeling temperature and precipitation variance: Beaudrot et al., 2019), the potential for interactions between temperature and precipitation effects (Ozgul et al., 2017), and distinguishing trends in the wetness of wet seasons from the dryness of dry seasons (Chou et al., 2013).

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Chapter 5: Conclusion

Nonhuman primates may be particularly vulnerable to the effects of rapid climate change, but the high frequency of fragmented habitats and a lack of long-term data have hampered our ability to observe their potential range of responses to climate change. Until this dissertation, no empirical evidence had demonstrated the often-predicted shifts of primate ranges along elevational gradients. Overall, the chapters in this dissertation provide four main findings: first, knowledge of the effects of contemporary climate change on nonhuman primates is disproportionately low, unevenly distributed, and often does not contextualize predicted effects on primates within changes in their biological environments. Secondly, primates are experiencing an ongoing range shift along an elevational gradient, although the extent and character of these range shifts are mediated by species' home range size. Thirdly, local weather conditions are not the primary cause of these shifts. Fourth, weather trends along the elevational gradient in Gunung Palung National Park are inconsistent with widespread increases in temperature and aridity across Borneo.

Far less is known about the effects of climate change on extant tropical species than those in temperate ranges (Beaudrot et al., 2018; Graham et al., 2016). However, climate change-induced extinctions have already been documented in the tropics (Pounds et al., 1999), and will potentially drive hundreds of species more towards extinction by 2050 (Thomas et al., 2004). Findings from this dissertation enrich our understanding of threats to extant primate populations and inform predictions of future change. For example, when accounting for food availability,

both temperature and precipitation were reliable predictors of primate abundance, reinforcing the importance of accounting for species' abiotic and biotic environments when projecting range shifts (Araújo & Peterson, 2012; Post, 2013). However, these relationships were rare, and neither local weather nor food availability were primary drivers of population dynamics over fourteen years. This suggests that accurately projecting future change of populations on fine-grained scales may necessitate additional ecological parameters often excluded from species distribution models (Santini et al., 2021), and predictions would benefit from knowledge of interactions among ecological and anthropogenic factors (Brodie, 2016).

Tropical endotherms such as primates are considered disproportionately vulnerable to rapid climate change and extreme weather events because Holocene environments were generally climatically stable in the tropics, thus modern tropical species may have evolved restricted environmental tolerances (Corlett, 2012). Findings from this dissertation show that primates at the Cabang Panti Research Station (CPRS) in Gunung Palung National Park are not declining due to increased temperatures, at least in part because local maximum temperatures are generally not increasing at CPRS. Further, counts of orangutans were positively associated with minimum temperatures, indicating that any direct impacts of weather on primates along the CPRS elevational gradient were more likely due to cool temperatures, rather than heat stress. Future work can profitably address whether primate behavior is affected by these local climate trends (e.g. modulating resting time [Korstjens et al., 2010] or increased huddling [Eppley et al., 2017]), which may be expected even more so than distribution shifts given primates' extensive, evolved behavioral repertoires. Future studies should also continue to focus on identifying causal drivers of abundance trends, specifically whether changes in abundance are related to climate in ways that our analyses did not account for (e.g. secular changes in extreme conditions), and the

influence of other ecological (e.g. additional kinds of species interactions, such as competition with other vertebrates) or anthropogenic processes (e.g. hunting, selective logging, fires).

While our results suggest that local climate conditions were not the primary driver of trends in primate distribution patterns at CPRS, we also show that most species' populations have declined over a relatively short period of time. Complex social networks and dietary flexibility buffer primate populations from environmental stochasticity (Morris et al., 2011), but demographic studies also indicate that long-lived species with slow reproductive rates, such as primates, are slow to recover from severe disturbances (Mitani, 1990). Indeed, rapid population declines on short timescales are not unprecedented, both globally (Estrada et al., 2017) and in Southeast Asia. Bornean orangutans are estimated to have declined by 25% over just a 10-year period between 2007-2017 (Santika et al., 2017), and within a protected area in Myanmar, hoolock gibbon (*Hoolock leuconedys*) group densities have declined by over 50 percent in just 16 years, from 2005-2021 (Tun et al., 2023). Additional demographic studies on primates at CPRS are needed to characterize how trends in counts at CPRS may be due to changes in encounter rates as opposed to true changes in habitat-specific carrying capacities, and how abundance declines may affect population viability. Such investigations are critical to determine whether ongoing distribution shifts may be successful evolved strategies for populations over these rapid timescales.

The nature of such rapid timescales influences the applicability of these findings to primate evolutionary history. In general, the precise biological effects of environmental changes are difficult to extract from the fossil record. Thus, anthropologists often rely on modern analogues to apply ecological perspectives to evolutionary frameworks (Kay, 1984; Nunn & van Schaik, 2002). Because populations at CPRS are experiencing ongoing range shifts over just

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several decades, our results support indications from the fossil record that that elevational

gradients could be useful climate refugia during periods of short-term climatic volatility in

species' evolutionary histories (Davis & Shaw, 2001). However, to make evolutionary

applications more tractable, future studies would benefit from considering the multidecadal

changes we describe in wider temporal contexts, such as millennial-scale progressions in the

Australian Monsoon climate system (Krause et al., 2019).

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Appendix I

Table A1. Description of data collected in the primate climate change database, Chapter 2. "Abbreviated Column Name" matches the column name in the header row of the full database (see Supplemental Information, Table S1: https://onlinelibrary.wiley.com/doi/full/10.1002/evan.21874).

Abbreviated Column Name	Full Column Name	Description/Scoring Options	Question/Explanation
manuscript_num	manuscript number	number	NA
editor	editor	names	NA
author	author	names	NA
title	title	manuscript title	NA
year	year published	year	NA
keywords	author keywords	author keywords	NA
primates	vertebrates studied are exclusively primates	yes/no	Are primates the only focal species of the study?
num_primates	number of extant primates with quantitative data	number	The number of focal primate species per study. A focal primate is either used in quantitative analysis (but see "basal_tax" for exceptions) or frames the main subject matter of the paper, even if the paper does not include data on the primate itself (e.g. Chapman et al.2: changes in primate community structure). A specific primate simply used as an example in the text is not counted as a focal primate. Each focal primate species is described in a separate row in the database (Supplemental Spreadsheet; see "basal_tax" for exceptions).
common_name	species common name	names	Taxonomy follows Estrada et al.3
tax_cat	broad taxonomic category	Ape, Lemur, Tarsier, OWM, NWM, Loris, NA	Separates species into broad taxonomic categories. OWM = Old World Monkey; NWM = New World Monkey

basal_tax	basal taxonomic level	If applicable, any taxonomic group that encapsulates the diversity of the manuscript's focal primates.	Identifies large-scale papers for which the taxonomic group(s) present are not represented by specific focal primate species (e.g. the basal taxonomic group "Catarrhini" within Nadler & Roos4). Used in cases where "tax_cat" = NA but either 1) analysis on specific primates does not combine an independent variable "time" with climate predictors (e.g. Estrada et al.3), or 2) there is a specific geographic focus (e.g. Nadler & Roos4). For each of these studies, the specific focal primates within the paper (if present) are not included in phylogenetic analyses. If there is a geographic focus, the paper is included in geographic analyses, although the entire paper appears as one data point (rather than a separate data point for each individual primate).
genus	genus	name, if applicable	Genus for each focal primate. Taxonomy follows Estrada et al.3. In cases of taxonomic discrepancies between a paper and Estrada et al., we note both designations in the Supplemental Spreadsheet. Our analyses use taxonomy consistent with Estrada et al.
species	species	name, if applicable	Species for each focal primate, if applicable (some studies are only specific to the genus level).
subspecies	subspecies	name, if applicable	Subspecies for each focal primate, if applicable. Note that taxonomy in Estrada et al.3 does not include subspecies designations. Therefore, any subspecies distinctions in our analyses are only as they appear in the original studies.

IUCN	IUCN status	IUCN Red List categories: "LC" (Least Concern), "NT" (Near Threatened), "VU" (Vulnerable), "EN" (Endangered), "CR" (Critically Endangered), "DD" (Data Deficient)	For focal primates only. IUCN designations are consistent with www.iucnredlist.org as of February 2019. If the focal primate subspecies is not represented on the IUCN Red List, the subspecies inherits its parent species' designation (see Supplemental Spreadsheet). NA if the study has no listed focal primates.
geo_region	geographic region	Africa, Madagascar, Asia, South America, Captive, or Semi-wild	Broad geographic region inhabited by the focal primates. "Captive" designates studies that were done in captivity, and "semi-wild" refers to data collected on Cayo Santiago with semi-wild Rhesus Macaques.
country1: country10	country 1: country 10	countries	Country where focal primate data were collected. Columns 1:10 are present to accommodate studies for which focal primate data spans multiple countries. Not applicable for studies without focal primates, or if focal primates inhabit multiple countries and the provenience of the primate data was not readily accessible (e.g. Korstjens et al.5)
cc_title_key	Does "climate change"/"global warming" appear in the title or keywords?	yes/no	"Are the terms "climate change" or "global warming" in the study's title or keywords? (Variants of these terms, such as "climate variations"," climate fluctuations", or use of the term "environmental" instead of "climate", were excluded)

cc_framing	"climate change"/"global warming" appears neither in title nor keywords, and not more than once in intro and/or discussion	yes/no	Is climate change used to frame the study without being the focus of the study? To meet this condition, the terms "climate change" or "global warming" do not appear in the study's title or keywords, and also do not appear more than once in the study's introduction or discussion. The phrases were found by searching the keyword roots "climat" and global" through the manuscript text. We accepted slight variations of the terms at our discretion, for example "change in climate."
cc_title_key_only	"climate change"/"global warming" appears in the title or keywords, but only reappears at most once in the intro and/or discussion	yes/no	Is climate change discussed in papers that self-identify as climate change research? To meet this condition, the terms "climate change" or "global warming" are in the paper's title or keywords, but do not appear more than once in the introduction or discussion of the text. The text of each study was searched with the same method as the "framing_filter".
time_broad	past (premodern) or contemporary	past, contemporary, both	This condition identifies the timescale of the study: are the analyses (or discussion, if no quantitative analyses) using data from primates in the past, primates in modern times, or both? With this variable, we distinguish studies that focus on anthropogenic climate change as opposed to climate change on an evolutionary timescale. Post6 distinguishes "recent" climate change as changes that have occurred since the Industrial Revolution; therefore, we draw the line between past and contemporary at the Industrial Revolution or 1800 A.D. Because our review focuses on anthropogenic climate change, all analyses in this study exclude "past" studies.

past_time	if past, what target time?	geologic epochs (except for Zhao et al., 2018: c.a. 1000BP-present)	If the focal timescale of the study met the condition "past," what specific time was targeted?
cc_qual	qualitative climate change	yes/no	One of the two main conditions to determine if the study is a "climate change" study. To be a qualitative climate change paper, the paper must substantively discuss how human-driven climate change affects primates but not meet our criteria for a quantitative study (see next row). We assessed this this by searching the keyword roots "climat" and "global." If, in a primate context, the text lends explicit discussion of climate change, we scored "yes" for this condition. This condition is necessary to ensure that clearly relevant studies such as Korstjens & Hillyer7 are scored as climate change studies even in the absence of any quantitative analysis of focal primates. A notable instance of where this condition is not met is where "climate change" or "global warming" appear repeatedly in the text but only refer to climate change as a potential threat to primates (e.g. Brncic et al.8)

| cc_quan | quantitative climate change | yes/no | The second main condition to determine if the study is a "climate change" study. To meet this condition, a paper must satisfy two criteria: chronological time is an independent variable in the representation of focal primate data (whether descriptive [e.g. Brncic et al.8] or shows the results of an analysis), and some abiotic climate variable (e.g. temperature, precipitation) was used as a predictor (or outcome) variable in the same analysis. Because we did not set a minimum duration on elapsed time, analyses with very limited timeframes still qualified (e.g. winter and summer comparison with 6 months' elapsed time10) The "chronological" requirement excludes studies that meet the "temporal_binned" condition. |
| primate_temporal | primate_temporal | yes/no | This is the first of four categories used to describe temporal analyses. For a dependent variable to be a "primate" variable, the unit of change must be some intrinsic primate quality. These include units pertaining to demography, life history, disease, morphology, isotopes, population, behavior, and physiology. |

food_temporal	food_temporal	yes/no	This is the second of four categories used to describe temporal analyses. To meet this condition, the dependent variable of focal primate analyses needs to present some trend in important primate food sources over time (e.g. phenology, nutrition or mechanical properties of food). Primate feeding data are scored as "primate" rather than "food" dependent variables, since the measured change is a primate quality rather than something intrinsic to the food source itself. Notably, in order for our literature search to return a study that focuses exclusively on food, the study would have to include specific primate names in the text. We are cognizant of the fact that there are studies that describe important primate food sources without mentioning any primate nomenclature, and those studies were not included in this review.
hab_temporal	habitat_temporal	yes/no	This is the third of four categories used to describe temporal analyses. In this condition, the dependent variable of focal primate analyses shows some trend in primate habitat over time (e.g. habitat suitability, forest cover).
other_temporal	other_temporal	yes/no	This is the last of four categories used to describe temporal analyses. This is a "catch-all" category for which the dependent variable of a temporal analysis cannot be binned into one of the first three categories, but nevertheless is undoubtedly relevant for primates. These include climate itself (e.g. observed trends in precipitation through time11) and changes in primate pathogens.

primate_spatial	primate_spatial	yes/no	This is the first of four categories used to describe spatial analyses. Examples of spatial analyses include habitat comparisons, altitudinal gradients, and species distribution models. While these analyses often include data that were collected over a period of time (e.g. Camaratta et al.12), the analyses themselves do not assess changes through time. For this reason, we did not include studies that only included spatial analyses in our descriptive analyses.
food_spatial	food_spatial	yes/no	This is the second of four categories used to describe spatial analyses. The dependent variable is primate food (see "food_temporal")
hab_spatial	hab_spatial	yes/no	This is the third of four categories used to describe spatial analyses. The dependent variable is primate habitat (see "hab_temporal")
other_spatial	other_spatial	yes/no	This is the last of four categories used to describe spatial analyses. The dependent variable is some "other" variable (see "other_temporal")
ext_weather	extreme weather events	yes/no	This category further describes temporal and spatial analyses. For this condition to be met, an extreme weather event must be explicitly relevant to, or otherwise frame, the quantitative analysis (e.g. comparison of primate populations before and after a hurricane13).
abiotic_primate	direct effect of abiotic factors on primate physiology	yes/no	This category further describes temporal and spatial analyses. For this condition to be met, a quantitative analysis tests how an abiotic climate variable directly influences primate physiology (e.g. core body temp)

phylo_genetic	primate phylogenetic reconstruction/genetic analyses	yes/no	This category further describes temporal and spatial analyses. For this condition to be met, the quantitative analyses are either phylogenetic reconstructions or describe specific genes over time or space.
disease_microbiome	disease/health	yes/no	This category further describes temporal and spatial analyses. For this condition to be met, the analysis must focus on a primate pathogen, the effect of a pathogen on primates, or the primate microbiome.
temporal_chron	temporal data: observed secular change over time	yes/no	This is the first of four conditions that qualifies the four categories (primates, habitat, food, or "other") of temporal studies. For this condition to be met, there must be an observed trend in the dependent variable over chronological time.
temporal_future	temporal data: predicted future change over time	yes/no	This is the second of four conditions that qualifies the four categories (primates, habitat, food, or "other") of temporal studies. For this condition to be met, the change in the dependent variable is a prediction about future change.
temporal_past	temporal data: predicted past change	yes/no	This is the third of four conditions that qualifies the four categories (primates, habitat, food, or "other") of temporal studies. For this condition to be met, the change in the dependent variable is a prediction about the past (e.g. hindcasting, phylogenetic analyses, and comparative morphology of fossils).

temporal_binned	temporal data: non-secular	yes/no	This is the last of four conditions that qualifies the four categories (primates, habitat, food, or "other") of temporal studies. For this condition to be met, the change in the dependent variable has lost chronological resolution (e.g. Frasier et al.14)
start_year_primate	year start (primate)	year	The year that primate data collection started (for "temporal_chron" and "temporal_binned" data).
end_year_primate	year end (primate)	year	The year that primate data collection ended (for "temporal_chron" and "temporal_binned" data).
elapsed_primate	elapsed time, primates (years, rounded up)	number	Elapsed time between the start and end of primate data collection. This number is accurate to within the reported timeframe in the paper's methods. For example, if the month is not reported, years are rounded up (data collected between 2001 and 2003 = three years).
start_year_food	year start (food)	year	The year that food data collection started (for "temporal_chron" and "temporal_binned" data).
end_year_food	year end (food)	year	The year that food data collection ended (for "temporal_chron" and "temporal_binned" data).
elapsed_food	elapsed time, food (years, rounded up)	number	Elapsed time of food data collection. This number is accurate to within the reported timeframe in the paper's methods. For example, if the month is not reported, years are rounded up (data collected between 2001 and 2003 = three years).
start_year_hab	year start (habitat)	year	The year that habitat data collection started (for "temporal_chron" and "temporal_binned" data).
end_year_hab	year end (habitat)	year	The year that habitat data collection ended (for "temporal_chron" and "temporal_binned" data).

elapsed_hab	elapsed time, habitat (years, rounded up)	number	Elapsed time of habitat data collection. Accurate to within the reported timeframe in the paper's methods. For example, if the month is not reported, years are rounded up (data collected between 2001 and 2003 = three years).
temp_data_continuous	observed temporal data: continuous	yes/no	For cases where "temporal_chron" or "temporal_binned" are met. For this condition to be met, data were collected continuously throughout the study period.
temp_data_discrete	observed temporal data: discrete	yes/no	For cases where "temporal_chron" or "temporal_binned" are met. For this condition to be met, data were collected in discrete, disconnected timeframes throughout the study period (e.g. Chapman et al.15: comparison of protozoan infections in primates from between 1979 and 2012).
discrete_times	discrete times	times	If the condition "temp_data_discrete" was met, this condition describes those specific times.
conserv	"conserv" appears at least twice in either the introduction and/or the discussion	yes/no	Does the study discuss primate conservation? For this condition to be met, the word "conservation" (or a similar word, e.g. "conserves," "conserved," etc.) must appear at least twice in the introduction and/or discussion. To evaluate this, we searched for the keyword root "conserv" and observed the context in which the word was used. The word must be used in a primate conservation context (e.g. "variability was conserved" would be excluded).

evol	"evol" appears at least twice in either the introduction and/or the discussion	yes/no	Does the study discuss primate evolution? For this condition to be met, the word "evolution" (or a similar word, e.g. "evolve," "evolves," etc.) must appear at least twice in the introduction and/or discussion. To evaluate this, we searched for the keyword root "evolv" and observed the context in which the word was used. The word must be used in a primate evolution context (e.g. "our thinking has evolved" would be excluded).
SDM	species distribution model/MaxEnt	yes/no	Do the authors perform species distribution modelling? We define Species Distribution Models according to Elith & Leathwick.16
Maxent	MaxEnt	yes/no	If the "SDM" condition is met, does the modeling use the MaxEnt software?