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The status of primates and primatology in Myanmar

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ABSTRACT

Myanmar is one of the world's most biologically rich countries and has among the largest contiguous intact forest landscapes in southeast Asia. Yet many of its ecosystems are highly threatened and there is an urgent need for greater wildlife conservation action, particularly for its 20 primate species, over half of which are either Endangered or Critically Endangered on the IUCN Red List of Threatened Species. Of these 20 species, three survive in small, isolated populations, while for the remaining 17 there is insufficient population and distribution information to accurately target conservation management and monitoring. To begin to address this challenge, we conducted semi-structured interviews with senior academics and professionals working in primate conservation in Myanmar to assess current knowledge on the conservation status of each of the primate species found there, as well as conservation efforts underway. We also conducted a systematic literature review to generate data on publication metrics for Myanmar primatology. The principal finding is that the populations of nearly all of Myanmar's 20 primate species are declining, and there are gaps in knowledge on species population dynamics which are

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Table 1A summary of the 20 species of primate found in Myanmar.

Common Name	Scientific Name	IUCN Red List Status	Distribution	Population Size and Trend	Threats	Reference (s)
Slow loris Bengal slow loris	Nycticebus bengalensis	Endangered	Widespread across Bangladesh, Bhutan, Cambodia, China, India, Lao People's Democratic Republic, Thailand, Vietnam and Myanmar. In Myanmar, it is found nationwide, most notably in Bhamo, Sumprabum, Mindat, Chin Hills, Pathein, Thaungdaung, Pegu, and the Mergui Archipelago.	Although widespread, the exact population size in Myanmar is unknown. The overall population is decreasing.	Habitat loss, degradation, and fragmentation due to slash and burn cultivation, expansion of tea plantations, illegal logging, illegal hunting, road accidents, forest fires, and linear infrastructure cutting across habitats. Also threatened by exotic pet trade and used in traditional medicines. Commonly sold in markets, as well as hunted for food.	ICIMOD (2021) Nekaris et al. (2020) Nijman et al. (2014)
Langur monkey						
Popa langur	Trachypithecus popa	Critically Endangered (assessment in progress)	Endemic to Myanmar. It is found between the Ayeyarwaddy and Thanlwin rivers in central Myanmar, and the western foothills of the Kayah- Karen Mountains.	199–259 individuals. Trend is unknown, but likely to be decreasing.	Hunting, habitat loss, degradation, and fragmentation caused by agricultural encroachment, illegal/unsustainable timber extraction, and disturbances caused by collection of non-timber products and free cattle grazing.	Roos et al. (2020)
Phayre's langur	T. phayrei	Endangered	Distributed in Bangladesh, India as well as Myanmar. It is located west of the Chindwin and Ayeyarwaddy rivers.	Unknown in Myanmar due to insufficient information available. The overall population is decreasing.	Habitat destruction due to logging, encroachment, slash and burn cultivation, and monoculture forest plantation. It is also threatened by hunting and trade in wildlife parts.	Roos et al. (2020) ICIMOD (2021) Chetry and Ahmed (2021
Shan State langur	T. melamerus	Endangered	Found on the Shan Plateau and in neighboring China, between the Ayeyarwaddy and Thanlwin rivers. This species' southwestern range likely extends into the Kayah-Karen Mountains.	Unknown in Myanmar due to insufficient information available. The overall population is decreasing.	Unknown.	Roos et al. (2020) Bleisch et al. (2020)
Tenasserim lutung	T. barbei	Vulnerable	Found in Thailand and Myanmar. In Myanmar, there are accounts from the Tanintharyi Region, Myintmoletkhat Range and forested area along the Ngawon and Laynyar rivers.	Unknown due to insufficient information available. The overall population is likely to be decreasing.	Habitat destruction and hunting for food and medicine.	WCS, unpublished data Nadler (2021
Dusky langur	T. obscurus	Endangered	Found in Malaysia, Thailand and Myanmar. In Myanmar, it is located in the south in Mon, Kayin and Tanintharyi States, and the Mergui Archipelago.	Unknown in Myanmar due to insufficient information available. The overall population is decreasing.	Hunting for food and habitat loss and degradation, mainly due to expanding oil palm plantation, agriculture and urbanization.	WCS, unpublished data Roos et al. (2014) Boonratana et al. (2020a)
Indochinese gray langur	T. crepusculus	Endangered	Found in Cambodia, China (Yunnan), Lao People's Democratic Republic, Thailand, Vietnam and northern Myanmar. Limited information on	Unknown in Myanmar due to insufficient information available. The overall population is decreasing.	Limited information on threats in Myanmar.	Yongcheng et al. (2021)

Table 1 (continued)

Common Name	Scientific Name	IUCN Red List Status	Distribution	Population Size and Trend	Threats	Reference (s)
			specific localities in			
Shortridge's langur	T. shortridgel	Endangered	Myanmar. Found in southwestern China (Yunnan) and northeastern Myanmar. In Myanmar, it is found south of the Hukaung valley, east of the Chindwin river.	Unknown due to insufficient information available. The overall population is likely to be decreasing.	Habitat loss and destruction due to illegal logging, deforestation for agriculture and timber, and extraction of nontimber forest products. Also threatened by hunting and trade in wildlife parts.	ICIMOD (2021) Long and Htun (2020)
Capped langur	T. pileatus	Vulnerable	Found in Bangladesh, Bhutan, China, India and Myanmar. In Myanmar, it is found west of the Chindwin river in the Chin Hills south to Mount Victoria.	Unknown in Myanmar due to insufficient information available. The overall population is decreasing.	bestruction of forest habitat for fuel wood collection and timber extraction, forest encroachment for slash and burn cultivation and tea plantations, and illegal hunting for meat and trade.	ICIMOD (2021) Das et al. (2020)
Robinson's banded langur	Presbytis robinsoni	Vulnerable	Found in Indonesia, Malaysia, Singapore, Thailand and southern Myanmar. Limited information on specific localities in Myanmar.	Unknown due to insufficient information available. The overall population is likely to be decreasing.	Deforestation and conversion of habitat, especially for monoculture crops.	Ang and Boonratana (2020)
Snub-nosed mon	ikey Rhinopithecus	Critically	Found in China and	A	Logging and construction	37:4 -1
Myanmar snub- nosed monkey	strykeri	Endangered	Myanmar. In Myanmar, it has a very limited distribution (560 km²) on the Salween-N'mai Hka divide in northeastern Kachin state. Found in montane forests and watershed area of the Maw river, a tributary to the N'mai Hka river, as well as forests to the east of the Chichitago village.	Approximately 300 individuals in Myanmar. The overall population is likely to be decreasing.	of camps has led to an increase in demand for bush meat and wildlife trade. Habitat destruction due to the extraction of non-timber forest products, medicinal plants.	Yin et al., unpublished data Geissmann et al. (2011) Geissmann et al. (2020) ICIMOD (2021)
Rhesus macaque	Macaca mulatta	Least Concern	Found throughout most of southern Asia. In Myanmar, it is mostly found north of Yangon.	Unknown population size and trend across its range.	Illegal hunting and trade. Habitat destruction by logging, encroachment, slash and burn cultivation, and monoculture forest plantations. Also threatened by dog predation and the pet trade.	ICIMOD (2021) Singh et al. (2020)
ong-tailed macaque or Crab- eating macaque	M. fascicularis	Endangered	Widespread across southern Asia. In Myanmar, it is located in Rakhine and southern Tanintharyi regions, as well as the Ayeyarwady Delta, and Bago Yoma.	11,130–107,900 individuals. The overall population is likely to be decreasing.	Habitat loss from logging, agricultural and aquaculture farming, as well as hunting for food and trade.	San and Hamada (2011) Eudey et al. (2021)
Stump-tailed macaque	M. arctoides	Vulnerable	Widespread across southern Asia. It is found in northern Myanmar.	Unknown in Myanmar due to insufficient information available. The overall population is decreasing.	Habitat destruction due to logging and encroachment for agriculture. Illegal hunting.	Chetry et al. (2020) ICIMOD (2021)
Assamese macaque	M. assamensis	Near Threatened	Found in Bangladesh, Bhutan, China, India, Lao People's Democratic Republic, Nepal, Thailand, Vietnam and Myanmar.	Although it is a very common species, the population size is unknown in Myanmar.	Habitat destruction by logging, encroachment, and slash and burn cultivation, and monoculture forest	Boonratana et al. (2020b ICIMOD (2021)

(continued on next page)

Table 1 (continued)

Common Name	Scientific Name	IUCN Red List Status	Distribution	Population Size and Trend	Threats	Reference (s)
			Found in northern and eastern Myanmar.	The overall population is likely to be decreasing.	plantations. Illegal hunting and trade is also a threat.	
Northern Pig- tailed macaque	M. leonina	Vulnerable	Widespread across southern Asia. Found in central and northeastern Myanmar, including the Mergui Archipelago. Recorded on the coast of Arakan.	Although it is a very common species, the population size is unknown in Myanmar. The overall population is likely to be decreasing.	Habitat destruction due to logging and encroachment for agriculture. Illegal hunting.	Boonratana et al. (2020c ICIMOD (2021)
Gibbon (Small	•					
Western hoolock gibbon	Hoolock hoolock	Endangered	Found in Bangladesh, India (Assam) and Myanmar. In Myanmar, it is located west of the Chindwin and Ayeyarwaddy rivers, along the Rakhine Yoma, northern Rakhine state boarding Bangladesh and Naga Land.	At least 30,000 individuals. The overall population is likely to be decreasing.	Habitat loss, degradation, and fragmentation due to slash and burn cultivation, tea plantation expansion, extraction of non-timber products and agricultural encroachment. Hunting for both meat and for use in traditional medicines.	Geissmann et al. (2013) Brockelman et al. (2019) ICIMOD (2021)
Eastern hoolock gibbon	H. leuconedys	Vulnerable	Presence uncertain in India. In Myanmar, it is found east of Chindwin and Ayeyarwaddy rivers.	At least 60,000 individuals. The overall population is decreasing.	Habitat loss, fragmentation, mining, and degradation due to commercial logging, shifting cultivation, rotational agriculture, tea plantation expansion, timber extraction, and road construction. Illegal capture for trade is also a threat, as well as hunting, both for meat and for use in traditional medicines.	Brockelman and Geissmann (2019) ICIMOD (2021) Brockelman et al. (2020)
Skywalker gibbon	H. tianxing	Endangered	Found in China. Locality information in Myanmar is uncertain, but likely to be located east of Ayeyarwaddy and N'Mai Kha rivers. Historical museum specimens were found in Gokteik and Shan States, northern Myanmar.	Myanmar numbers currently unknown, but 150 individuals on the border with China. The overall population trend is decreasing.	Habitat degradation, fragmentation, and loss due to encroachment of forest for settlement, agriculture, and livestock grazing. Illegal hunting for food, medicine, and trade is still prevalent. An isolated and fragmented population size poses an additional threat.	Fan et al. (2017) Fan et al. (2020) ICIMOD (2021)
Lar or white- handed gibbon	Hylobates lar	Endangered	Found in Indonesia (Sumatera), Lao People's Democratic Republic, Malaysia (Peninsular Malaysia), Thailand and Myanmar. In Myanmar, it is found east of the Thanlwin River in Shan, Kayah, Kayin, Mon states, and the Tanintharyi Region. Often located 1200 m above sea level.	Unknown in Myanmar due to insufficient information available. The overall population is decreasing.	Severe habitat loss due to land conversion for commercial plantation development.	WCS, unpublished data Brockelman and Geissmann (2020)

hindering conservation action. We present an overview of primatology in Myanmar and address the challenges and recommendations for the future of primate conservation in Myanmar.

1. Introduction

Myanmar is the second largest country in southeast Asia with one of the largest remaining tracts of contiguous forest, the Northern Forest Complex (totaling over 6.1 million hectares) (Bhagwat et al., 2017; Suarez-Rubio et al., 2020). The country is one of the world's

most biologically rich regions with highly threatened ecosystems and therefore an urgent priority for wildlife conservation (WCS, 2012). In total, the country supports 233 known mammals, including 20 species of non-human primate (primates hereafter) (WCS, 2012; FD, 2015; IUCN, 2021). Primates are considered keystone species, with their conservation often leading to the preservation of other species in their shared ecosystems (Campbell et al., 2011; Marshal and Wich, 2016). They are therefore considered key indicator species for habitat conservation success and can improve effective management of habitats (i.e., protected areas (PAs)) (Lwin et al., 2022; Tun et al., 2023).

In 2014, a study ranked 22 Asian countries according to the total number of primate species, and Myanmar was ranked seventh (Roos et al., 2014). Myanmar's 20 species of primate include: the Bengal slow loris, five species of macaque, nine species of langur, the Myanmar snub-nosed monkey, and four species of gibbon (Table 1; Figs. 1–4). Whilst nine of the primate species are widespread across southeast Asia, three have small, isolated ranges (i.e., Shortridge's and Popa langurs, and Myanmar snub-nosed monkey) (Fig. 2) (Long and Htun, 2020; Roos et al., 2020), and the remaining have insufficient data available for Myanmar to confirm population and range estimates (Table 1). The newly-described Popa langur (Roos et al., 2020) and eastern hoolock gibbon are the only primate species that are believed to be endemic to Myanmar; however, the latter species is thought to possibly occur in India (Brockelman et al., 2020). The newly described Skywalker hoolock gibbon (Hoolock tianxing) is also predicted to have extant populations in Myanmar (Fan et al., 2017, 2020; Lwin et al., 2021).

Fifteen out of the 20 primate species lack sufficient data to provide even approximate population estimates across Myanmar (Table 1), highlighting clear gaps in knowledge. Furthermore, populations of all species are thought to be declining, with 10% currently assessed as Critically Endangered, 50% Endangered, 30% Vulnerable, 5% Near Threatened, and 5% Least Concern (IUCN, 2021). Habitat loss, degradation and fragmentation, coupled with hunting (whether for trade or subsistence), appear to be universal threats impacting all 20 species of primate in Myanmar (Table 1) (IUCN, 2021).

Myanmar has a unique history, presenting diverse challenges and opportunities for safeguarding wildlife, notably primates, as they often depend on intact original forest habitats with buffers from surrounding human communities (Schwitzer et al., 2011). Rich in teak, minerals, oil and gas, Myanmar's forest landscapes have historically faced competition for human resources (McCarthy, 2000; Selmier, 2013). Despite this, Myanmar has retained large forests in the far north and south of the country (Bhagwat et al., 2017). Since 1981, national as well as international interest in wildlife conservation in Myanmar has been increasing, which led the Myanmar Forest Department to establish the Nature and Wildlife Conservation Division (NWCD) with the support of the Food and Agriculture Organization of the United Nations Development Program (FAO-UNDP) (FD, 2015). Country goals were identified to increase the PA systems by at least 5% in the short-term and 10% by 2030 (Rao et al., 2002; Myint Aung, 2007). Further political and economic changes were initiated in 2011 as the country moved towards democracy and economic deregulation (Hlaing, 2012), which resulted in

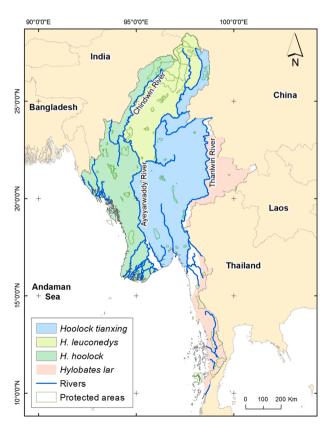


Fig. 1. Distribution of gibbon species (Hoolock and Hylobates) in Myanmar.

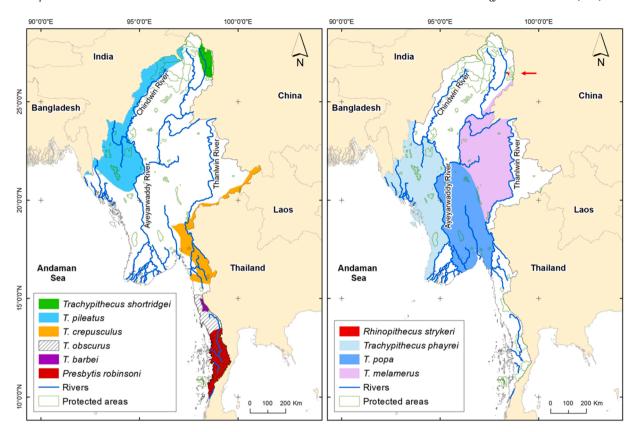


Fig. 2. Distribution of langur species (*Trachypithecus* and *Presbytis*) and Myanmar snub-nosed monkey (*Rhinopithecus stykeri*) in Myanmar. Distribution shapefiles for *T. barbei*, *T. obscurus*, *T. crepusculus*, *T. shortridgei*, *T. pileatus* and *P. robinsoni* downloaded from www.iucnredlist.org on 10 May 2023.

further reforms in 2015 and the lifting of U.S. economic sanctions, allowing for an influx of interest in Myanmar's biodiversity from the international community (Prescott et al., 2017). During this period, Myanmar increased collaboration with international conservation agencies and signed multiple Memoranda of Understanding (MoU) between related ministries and national and international non-governmental organizations (NGOs) to support conservation. Several MoUs were also signed between Myanmar and regional/international universities to support the improvement of higher education (primarily MSc and PhD level) (Personal Communication, Ngwe Lwin). However, the improved socio-political stability resulted in an acceleration of land conversion for commercial plantations, infrastructure development and tourism, and mining and energy – common trends associated with development (Zhang et al., 2018; Donald et al., 2015). Myanmar's engagement with the international community has changed drastically since the shift in political power in 2021 (Plunkett et al., 2022), with the focus changing to national led conservation efforts. The conservation outcomes of this shift are still waiting to be analyzed.

Myanmar also has a complex history of civil conflict, which has historically impacted conservation efforts. There are over 135 ethnic groups in Myanmar, demonstrating the cultural complexity of the country (Gravers, 2007). One of the major challenges facing primate conservation and research in Myanmar is that much of the intact forest complex habitat is in regions where there is ongoing civil conflict (Chow and Han, 2023). Established ethnic armed organizations (EAOs) operate in a "hybrid governance" structure where state and non-state authority intersect and overlap (South, 2018) and some EAOs have developed their own policies in support of forest management and conservation efforts within their land jurisdictions, in parallel to central government regulations (Personal Communication, Nature Conservation Society Myanmar). Conservation activities in Myanmar, particularly regarding primate habitats, must include a concerted effort to understand evolving domestic political tensions, and be aware of the local security situation in specific conservation areas. For example, at the time of writing this manuscript, foreigner's direct involvement in fieldwork in primate conservation areas is largely considered to be unsafe and foreign travel permissions are currently not being granted to these areas.

Despite these challenges, this is a critical time for primatology within Myanmar as the recent window of opening to the international community has fostered new interest among national researchers and students in studying primate conservation. Advancing expertise among national experts will allow for primatology research and conservation to continue despite changing international policies towards work in Myanmar. Baseline information is first required to guide future primatological research efforts. Therefore, this study aimed to highlight potential research gaps by investigating: i) the history and breadth of primate-based studies published on Myanmar primates (including focus species and regions, and the number of studies involving and/or first-authored by Myanmar nationals); ii) the cultural significance of primates in Myanmar and how this impacts their conservation; iii) on-going conservation

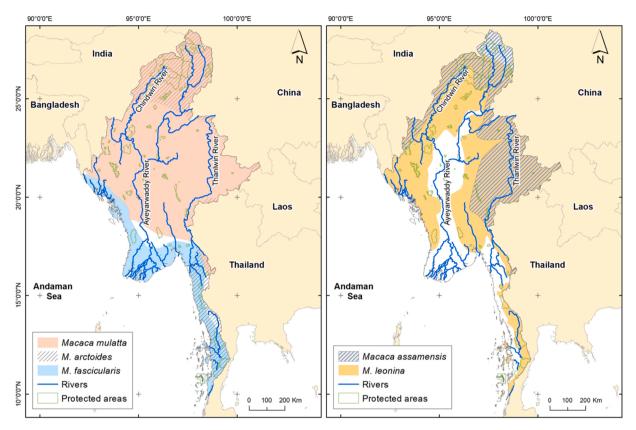


Fig. 3. Distribution of macaque species (Macaca) in Myanmar. Distribution shapefiles downloaded from www.iucnredlist.org on 10 May 2023.

efforts; iv) the current situation and obstacles faced by primate conservation professionals and students in academia in Myanmar; and v) recommendations for the future of the discipline in Myanmar.

2. Methods

We conducted a systematic literature review using standardized literature search guidelines known as PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyse) (Moher et al., 2009). A comprehensive summary of primatology literature from Myanmar and its international impact is yet to exist; therefore, this research tool was ideal for identifying, evaluating and summarizing the peer-reviewed literature in a systematic, non-biased way (Pullin and Stewart, 2006). To complement the review findings and include non-peer-reviewed or published sources, semi-structured interviews were carried out to evaluate data on primate distributions, population descriptions and conservation in Myanmar.

2.1. Systematic literature review

To generate data on publication metrics for Myanmar primatology, a systematic approach was taken in which a search was performed for article matches published between 01/01/1900 and 23/09/2021 in "All Databases" in Web of Science (WoS) and Google Scholar. This timeframe was chosen as WoS records start from 1900, and peer-reviewed primate research in Myanmar has been recorded from the first half of the 1900 s (Colbert and Brown, 1937). The search was expanded to "All Databases" in WoS to ensure publications in less accessible journals (e.g., *Journal of the Bombay Natural History Society*) and taxa-specific journals (e.g., *Gibbon Journal*) were included. There are currently no Myanmar-specific journals on biodiversity conservation or primatology, but the search did include Indian research collections (e.g., *Rare Animals of India*) which are known to contain studies in Myanmar.

The following search criteria were used:

[(TS=(primat* or monkey* or gibbon* or ape* or loris* or macaque* or lutung* or langur* or "leaf monkey*" or "leaf-monkey*")) AND TS=(Myanmar or Burma)]

Results were filtered by articles and reports only, thus excluding theses, chapters, supplementary material, abstracts and posters. Memoirs and field notes were captured in the reports, especially in earlier publications. Articles were excluded where primates were not the main focus (e.g., multi-taxa studies) as our aim was to concentrate specifically on primatology literature. Studies on Burmese (e.

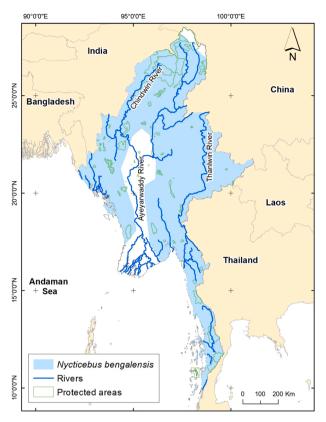


Fig. 4. Distribution of Bengal slow loris (*Nycticebus bengalensis*) in Myanmar. Distribution shapefile downloaded from www.iucnredlist.org on 10 May 2023.

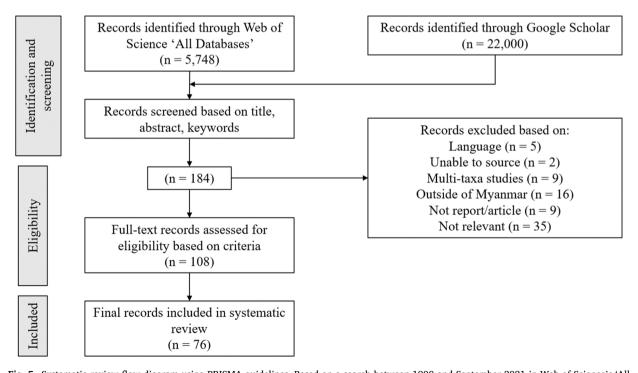


Fig. 5. Systematic review flow diagram using PRISMA guidelines. Based on a search between 1900 and September 2021 in Web of Science's 'All Databases' and Google Scholar.

g., Burmese long-tailed macaques) or border species (e.g., Sino-Myanmar species) that were only reported outside of Myanmar were also excluded as we were specifically interested in research coming out of Myanmar. An advanced search using the same terms was then carried out in Google Scholar. Results were again screened for articles and reports on primates in Myanmar. Duplicates with the WoS results were deleted. All articles were filtered by the English language. The collated literature was chronologically organized into a Microsoft Excel table (Supplementary Material 1).

2.2. Semi-structured phone interviews

To examine the current status of primatology in Myanmar, as well as to fully understand on-going conservation efforts, five anonymous semi-structured telephone interviews were conducted between January 2021 and January 2022. Interviews were conducted with primatology professionals who teach zoology and/or conservation science at the university level and conduct research on primates in Myanmar. Only five interviews were conducted due to the limited number of national professionals with primatology expertise in Myanmar. An informed consent script was first read to each participant and verbal consent was received. The interviews were structured around 22 questions on conservation- and primate-focused teaching, national and international primatology opportunities for students, and current primate research being undertaken in Myanmar (Supplementary Material 2). Data were analyzed thematically and qualitative data reported. All data collection methods and ethics were approved by the Institutional Review Board (IRB) at University of California Davis, United States (IRB #1863876–1).

3. Results

The results of the systematic literature review performed in WoS and Google Scholar identified 5748 and 22,000 articles, respectively, that met the search criteria. Once the articles had been screened for relevance, only 76 articles remained (72 journal articles, four reports) (Fig. 5), dating from 1937 to 2021, with majority of publications dated from 2000 onwards (Fig. 6).

3.1. History of primatology in Myanmar

Although the systematic review identified Colbert and Brown (1937) as the first publication on Myanmar primates, two additional studies which pre-date this were identified by co-authors. Both were species descriptions of extant primates: *Presbytis melamera* (= *T. melamerus*) and *Presbytis crepuscula* (= *T. crepusculus*) (Elliot, 1909), and *Pithecus shanicus* (= synonym of *T. melamerus*) (Wroughton, 1917). Publications pre-dating 1937 did not make the final list of relevant publications because they were not peer-reviewed and therefore were not found in WoS 'All Databases'.

The study by Colbert and Brown (1937) described an extinct species, *Amphipithecus mogaungensis*, from the Pondaung Formation, a 2 km-wide continental formation in central Myanmar, from which many important components of the world's primate fossil record have since been discovered (e.g., Colbert and Brown, 1937; Szalay, 1970; Maw et al., 1979; Ciochon, 1985; Jaeger et al., 1999; Jaeger et al., 2011; Takai et al., 2015; Jaeger et al., 2019; Takai et al., 2021). The Magway Region, the location of the Pondaung Formation, has been the focus of the majority of primate research coming out of Myanmar since the 1930 s (n = 42, 55%). The earliest known anthropoids are now thought to have come from this region with subsequent distribution into Africa (Jaeger et al., 2019).

Despite interest in primate-based research in Myanmar prior to 1960, most data are unpublished and exist only in reports in the archives of national universities and/or Myanmar Forest Department (personal communication, Prof. Aye Mi San). During the decadeslong period of international isolation, primate research and conservation were not prioritized due to the constraints of international aid and limited presence of primatologists in the country (Geissmann et al., 2013). Although the majority of research outputs identified in

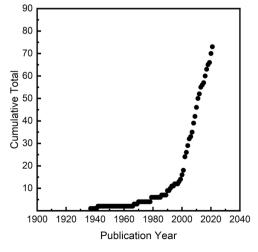


Fig. 6. Number of publications on Myanmar primates between 1900 and September 2021 (n = 76).

our study focused on fossil primates (51%), research has also been published on extant species including macaques (n = 13, 17%), hoolock gibbons (n = 11, 15%), snub-nosed monkeys (n = 6, 8%), and langurs (n = 3, 4%) (Fig. 7). The earliest published extant primate distribution record in Myanmar dates back to 1967 (Groves, 1967) where a series of skin specimens were used to confirm the distribution of the white-browed gibbon (*Hylobates hoolock*), now more commonly referred to as the western hoolock gibbon (*Hoolock hoolock*). Subsequently, the first direct observations of a primate species in Myanmar, of a langur species, occurred in 1990 (Choudhury, 1990).

The first known primate-focused population census and habitat assessment surveys were conducted on gibbons and carried out between 2004 and 2006 by the Myanmar Forest Department, Wildlife Conservation Society (WCS) and NWCD at the Mahamyaing Wildife Sanctuary and Hukawng Valley Tiger Reserves (Htun et al., 2006; Geissmann et al., 2013). Quantitative and comparable fixed point count acoustic sampling methods were used to estimate gibbon population density, whereby four listening posts were spaced 400–500 m apart and monitored for five consecutive days (Brockelman and Srikosamatara, 1993). A triangulation method was then used to determine the number of gibbon groups heard per day per listening post, and group density was calculated using a listening area radius of 1 km (assuming that all groups could be heard within 1 km from each listening post).

The first comprehensive hoolock gibbon status review began in 2008, funded by the Arcus Foundation Great Apes Fund, US Fish and Wildlife Service Great Ape Conservation Program and Gibbon Conservation Alliance (Geissmann et al., 2013), and was carried out by BANCA, FFI and PRCF, and incorporated work from WCS and KESAN, among others. This work established the most current understanding of the distribution of the then-known hoolock gibbon species in Myanmar (Htoo and Grindley, 2010). One of the contributing surveys by FFI and BANCA also led to the discovery of a new species, the Myanmar snub-nosed monkey (Geissmann et al., 2011).

Increasing effort has been placed on bringing knowledge of Myanmar primatology to the international community, as confirmed by the increase in publications since 2001. In 2010, FFI organised a symposium and workshop on hoolock gibbons during the 23rd Congress of the International Primatological Society (IPS) in Kyoto, where Myanmar primatologists presented the country's recent findings (Lwin et al., 2011).

3.2. Cultural significance of primates in Myanmar

Human-wildlife interactions are strongly impacted by cultural values and ideologies of nature, with local communities and ethnic groups connected to their natural world through locally-specific value systems (Infield et al., 2018). Humans and primates, most notably monkeys, have shared a rich cultural history across Myanmar. Although this is not heavily documented in academic literature – no relevant articles documenting shared cultural history were found in the systematic review – there are traditional folktales and taboos that have been passed down through the generations (Aung et al., 2021; Pyae Phyo Aung, personal communication). For example a Shan ethnic folktale of the "Monkey and the Crocodile", tells the story of a cunning monkey who outsmarts a crocodile, showcasing them as intelligent animals:

There were a pair of crocodiles. One fell ill, so the other went in search of a monkey heart cure. The searching crocodile came across a tree on a riverbank with lots of monkeys in it. Spotting a bold monkey jumping around, the crocodile tried to lure it onto its back with the promise of more fruit on the other side of the river. Eventually the monkey agreed. Once in the water, the crocodile began to sink, attempting to drown the monkey. When the monkey asked why, the crocodile explained it needed a monkey's heart. The monkey laughed and said that they do not travel with the their hearts because they are too heavy – they are

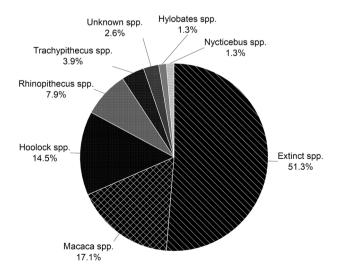


Fig. 7. The percentage of primate species coverage across publications (n = 76).

in fact hanging in a nearby tree. The monkey guided the crocodile back to shore and plucked two fig fruits (unbeknownst to the crocodile). Tricked, the crocodile took the fruit back to the other crocodile who ate them and instantly felt better.

-Shan ethnic folktale (Banyan Tree Reading Center, 2021)

Whilst monkeys hold cultural significance, so do apes, most notably gibbons. In neighbouring China, the gibbon has been recorded since the Zhou Dynasty (1027–221 B.C.) (van Gulik, 1967), where gibbons were described as "the aristocrat among apes and monkeys". Gibbons therefore are the subject of and have some of the most significant folk tales across Asia related to culture, religion and hunting taboos. In Myanmar, local communities often refer to them as "Myauk Ba Yin" or "Myauk Hwale Kyaw" in Burmese language, meaning "King of Monkey" (Aung et al., 2021). There appears to be a special regard for gibbons in Myanmar among the Kayin (= Karen), who have cultural taboos against killing gibbons because they believe this could result in the death of a family member or an agricultural disaster impacting their income and livelihood (Saw Moe San, personal communication). This special 'respect' for the species is thought to be due to observed similarities between gibbons and humans in the eyes of the Kayin (Saw Moe San, personal communication). Similar findings have been recorded on the Myanmar-China border in Yunnan province, China, where traditional ecological knowledge (TEK) and hunting taboos were found to limit poaching of gibbons, and therefore conservation strategies incorporating TEK into community-based efforts would aid gibbon survival (Zhang et al., 2020).

In other parts of Myanmar there is clearly a hunting culture that appears to be strongly linked to ethnicity despite government efforts to ban hunting in PAs (e.g., the Burma Wildlife Protection Act 1936). A recent report highlighted that the main objective of hunting primates was for subsistence, or to sell to neighbours or middlemen (Smiley Evans et al., 2020; Aung et al., 2021). Primates are thought to be targeted due to their large size and therefore their greater monetary value compared to smaller mammals. According to one recent study, a juvenile pet gibbon can fetch up to 80 USD, followed closely by a langur (6–7 USD/kg) and a macaque (4–5 USD/kg) for medicinal and food resources (Aung et al., 2021).

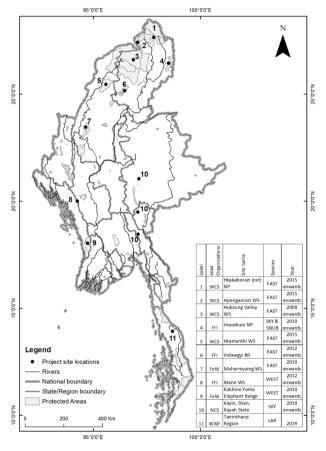


Fig. 8. Project sites of long-term primate conservation projects of national and international NGOs in Myanmar. All conservation projects have been collaborative in nature with 'Lead Organizations' collaborating with national NGOs. WCS = Wildlife Conservation Society; FFI = Fauna & Flora International; FoW = Friends of Wildlife; NCS = Nature Conservation Society; WWF = World Wildlife Fund. EAST = Eastern hoolock gibbon (Hoolock leuconedys); WEST = Western hoolock gibbon (Hoolock hoolock); SKY = Skywalker hoolock gibbon (Hoolock tianxing); SNUB = Myanmar snub-nosed monkey (Rhinopithecus strykeri); LAR = Lar gibbon (Hylobates lar).

3.3. On-going primate conservation efforts

Eighteen of the 20 primate species in Myanmar appear to have populations found both within and outside PAs (Figs. 1–4), thus highlighting gaps in conservation coverage. Only the Tenasserim lutung and Myanmar snub-nosed monkey fall within PAs (Fig. 2). Despite this, the Tenasserim lutung population estimates remain unknown due to insufficient information available, and both species' numbers are thought to be declining overall (Table 1). Furthermore, majority of langur species have unknown population sizes, and despite there being estimates for the Popa langur, the overall population trend is still unknown. The Bengal slow loris, lar gibbon, and rhesus, stump-tailed, Assamese and northern pig-tailed macaques also have unknown population sizes (Table 1). One of the challenges of primate conservation in Myanmar, is the lengthy process of declaring a PA and then actively implementing protection. For example, the proposed Lenya National Park in the south of the country is thought to potentially have seven primate species, yet after approximately 15 years of discussions to establish it as a PA, plans have still not materialised (Savini et al., 2022).

In Myanmar, both international and national conservation NGOs (e.g., FFI, WCS, People Resources and Conservation Foundation (PRCF), BANCA, FoW, and Wapalaw Wildlife Watch) have had long-term primate conservation projects running for the last 15 years (Geissmann et al., 2013; Fig. 8). Three out of the 11 projects have operated outside of PAs, focusing their conservation efforts on Skywalker, western hoolock and lar gibbons. In terms of collaborations, among the 76 Myanmar primate studies identified in the systematic review, 43 (57%) involved international collaborations with Myanmar researchers. At the time of writing, FFI, WCS, FoW, World Wildlife Fund (WWF) and Nature Conservation Society-Myanmar (NCS) were undertaking primate conservation in Myanmar targeting hoolock gibbons, Myanmar snub-nosed monkeys, and langur species (Fig. 8). The main funders of primate conservation and research in Myanmar have historically included Arcus Foundation, Halcyon Land and Sea Fund, US Fish and Wildlife Service, Margot Marsh Biodiversity Foundation, Helmsley Charitable Trust, Mohammed bin Zayed Species Conservation Fund, and Critically Ecosystem Partnership Fund.

FFI has initiated projects on the Myanmar snub-nosed monkey at Imawbum National Park in northeast Myanmar, where a new PA was established for legal protection of this Critically Endangered species (FD, 2015). At Mann Wildlife Sanctuary on the Rakhine Yoma Mountain range, there is also a new PA with a proposed community-based initiative for protecting the western hoolock gibbon. FFI is also conserving what is believed to be the Skywalker hoolock gibbon, in northeast Kachin State. Here, FFI, together with Chances for Nature (CfN), are focussing on population and threat assessments, whilst also conducting community outreach work at Indawgyi Biosphere Reserve, and gibbon behavioral ecology monitoring. This project is being led by FFI Myanmar's Acting Country Director and the research aims to model the conservation status of the threatened hoolock gibbon throughout its range in Myanmar, with a particular focus on ranging patterns and implications for PA management within the Indawgyi Biosphere Reserve (Lwin et al., 2021, 2022). This project is a great example of how international interest in primates in Myanmar, particularly gibbons, has led to the development of national interest and capacity in primatology.

WCS established an eastern hoolock gibbon conservation project for population monitoring and community outreach at Hpongan Razi Wildlife Sanctuary, Hkakaborazi Southern Extension, Hukaung Valley Wildlife Sanctuary, and Htamanthi Wildlife Sanctuary (WCS Myanmar, 2019). FoW also has similar projects focusing on eastern hoolock population monitoring and threat assessments and community outreach work at Maharmyaing Wildlife Sanctuary, as well as at Rakhine Yoma Elephant Sanctuary, focusing on western hoolock gibbon conservation (Daw Khine Swe, FoW, personal communication).

WWF-Myanmar, together with the Karen Wildlife Conservation Initiative and Wildlife Asia project, have worked together to insulate power lines to protect lar gibbons in the forests of southern Myanmar where electricity lines installed for a new grid system expose gibbons to risk of electrocution (Freund et al., 2021). Recently, NCS together with UC Davis and the IUCN SSA initiated the Skywalker Gibbon Conservation Project to identify species distribution and threats in eastern Myanmar.

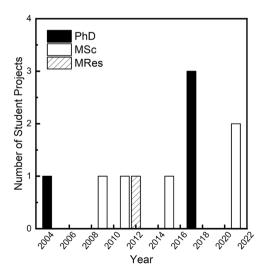


Fig. 9. The number of primate-related student projects in Myanmar between 2004 and 2021.

Of the 20 primate species in Myanmar, four species – the Myanmar snub-nosed monkey, western hoolock gibbon, eastern hoolock gibbon, and Skywalker hoolock gibbon – are being protected by both national and international conservation organizations. Apart from the long-tailed macaque, there are no targeted conservation interventions for the macaque species or the slow loris, even though they are considered threatened (IUCN, 2021). Previously, there was a langur conservation project at FFI between 2012 and 2013, but this has since been adapted to focus on the recently discovered Popa langur. Unfortunately, there is no specific conservation project for other threatened langur species. Of the four gibbon species found in Myanmar, there are no specific projects focused on the lar gibbon.

3.4. Primatology in Myanmar academia

Based on the semi-structured telephone interviews with five senior academics and primate conservation professionals, it is apparent that the Zoology Department at the University of Yangon is the leading insitution teaching wildlife conservation. The University of Yangon offers courses in mammology, animal behavior, ecology, molecular genetics, evolution, paleontology, and environmental studies and conservation, which include primate examples and concepts. The curriculum at the University of Yangon is duplicated across all other university institutions in Myanmar. Although anthropology departments and degrees exist, there are no degrees or modules focused specifically on biological anthropology or primatology (mirrored for the latter in China: Fan and Ma, 2018), but there is an option for course specialization within the zoology program. If a university student wants to pursue primatology they can select it as a "topic" for their studies, but this involves self-study and designing their research to align with their educational goals.

There have been 10 primate-based student projects (four PhD, five MSc, one MRes) conducted between 2004 and 2022, some of which are on-going (Fig. 9). These include two students from Myanmar who have conducted their studies with a university outside of the country. The 10 primate-based projects have focused on morphology, behavior, ecology and molecular genetics. Three primate species have been studied: long-tailed macaques, lar and eastern hoolock gibbons. Degrees in zoology at the PhD level are only offered through the University of Yangon and Mandalay University. The first primate-focused PhD was conducted between 2004 and 2007 by Professor Aye Mi San (now a retired professor of University of Yangon) who investigated the distribution, morphology/somatometry and behavior of long-tailed macaques. Between 2014 and 2018, Professor Aye Mi San went on to collaborate with the Primate Research Institute in Japan, investigating phylogeny in long-tailed and rhesus macaques (Prof. Aye Mi San, personal communication). At time of writing, there were two ongoing doctoral studies led by Yangon University; one on lar gibbons in Kayin State, and the other on long-tailed macaques in the Mawlamyine area (No No Wai, personal communication).

It was agreed amongst all academics and professionals interviewed that primatology and primate conservation needed to be further emphasized in the Myanmar academic system, and that primates generally fell behind other more charismatic species (e.g., tigers, elephants, and bears) in terms of conservation priorities within the country. One of the major impediments to university students pursing primatology research is the lack of national funding and the requirement to secure an affiliation with an international NGO or conservation group for resources given low national funding levels. Groups such as FFI have sponsored a staff member for their primate-related PhD research, which has provided simultaneous training to other staff members. There have also been opportunities through the Long-Tailed Macaque Project (www.theltmproject.org), in which four of Myanmar's senior primatologists are collaborators. While international collaboration is encouraged, the sustainability of securing academic opportunities through conservation NGOs was a concern among Myanmar academics interviewed. Another concern was the availability of qualified in-country supervisors in the field of primatology.

A gender gap in Myanmar was also recognized by academics interviewed. Although the number of women undertaking primatology and/or conservation field work is considerably greater than men in Myanmar, it was suggested that they encounter many obstacles in pursuing this academic direction, such as safety concerns with field work and the cultural taboo surrounding female students traveling to remote field sites with mostly male field teams, as well as safety concerns related to civil unrest in remote areas.

Internationally-led primatology research has been the norm across most of Myanmar's history, which was universally acknowledged in our interviews and evident in the results of our literature review. The first publication by a Myanmar national was not until 1979 (Maw et al., 1979), 70 years after the first publication on primates in Myanmar (which was by a foreign scientist: Elliot, 1909). Although Myanmar has revealed some of the largest primate ancestry discoveries of the 20th Century, only 13 of the 76 studies (17%) involved Myanmar researchers/institutions. Furthermore, only seven studies (9%) were first-authored by national researchers. This could be due to: a) the general nature of the university system in Myanmar where publishing is not encouraged or required in academic positions; b) a lack of international collaborations supporting national researchers (through funding and expertise); or also, c) a lack of opportunities for Myanmar researchers to gain experience publishing in competitive, international journals (Prof. Aye Mi San and Dr. Naw May Lay Thant, personal communication).

Simiarly, the interviewees revealed additional barriers due to a lack of accessible international primatology literature (due to high journal subscription), lack of internet access, primate-focused journals (e.g., International Journal of Primatology) not being relevant to the majority of formal degrees offered in Myanmar, and relatively high level of English language proficiency required to understand academic literature. Within Myanmar, there are a limited number of theses focusing on primatology which exist only in hard copy in Yangon, Myeik and Mawamyine university archives. Although it is difficult to know if other primate-based projects have gone unrecorded at different universities, the chances are small as primatologists in Myanmar are rare (Prof. Aye Mi San, personal communication).

4. Recommendations for the future of primatology in Myanmar

In general, conservation project actions, regardless of where they take place, need to use multiple, adaptive and locally driven conservation management approaches, including local leadership, integration of science and action, and capacity building and education to support on-the-ground conservation efforts that are informed by scientific monitoring and research (e.g., Schoneveld-de Lange et al., 2016; Biggs et al., 2017). In addition, projects need to ensure effective collaboration among multiple stakeholders, including government, local and international NGOs, and local communities.

Myanmar has made considerable progress in the field of primatology over the past 10 years, with an increasing number of students pursing advanced degrees undertaking primate-related projects. This momentum must be carried forward with a focus on advancing national training, research and conservation initiatives.

Within Myanmar, there are several stakeholders that need to consider knowledge gaps and barriers to the implementation of primate conservation research. These stakeholders include, but are not limited to, national and regional government, NGOs and universities. Some of the areas to address are listed below and are a combination of suggestions for stakeholders in Myanmar as well as for international collaborators supporting Myanmar primate conservation professionals and students.

4.1. Training gaps to fill within the Myanmar academic system

As highlighted in our interviews, there is a need for more university faculty and mentors in primatology within the Myanmar academic system. Currently, there are a limited number of experts with specialist knowledge in primatology in Myanmar who can teach and supervise student research. If we are to increase the number of students interested in pursuing graduate education related to primates, there needs to be appropriate support and guidance across disciplines including, but not limited to, zoology, anthropology and wildlife conservation departments/faculties. Suggestions for next steps are:

- Further collaboration among Myanmar universities and NGOs with those in other primate habitat countries and around the world to allow experts to contribute to the training and research development of primatologists in Myanmar. The reason being that the majority of work carried out on primates in Myanmar has not been by country nationals, and in the interests of including local ecological knowledge and decolonising conservation, more collaborations are needed. For example, in 2018, a transboundary Skywalker Gibbon Conservation Committee (https://skywalkergibbon.org) was founded with primate professionals from Myanmar, UK, US, Germany and China to conduct Skywalker gibbon habitat viability and population assessments in Myanmar. International professionals shared their expertise through online and in-person trainings with Myanmar nationals to aid with gibbon population surveying and estimation, and sample collection.
- Extramural funding for primatology research (Master degree level and above) as well as funding to support the operations of NGOs. With changing political relationships between Myanmar and the international community, resources available for primate conservation are dwindling. International funding can and should continue to be used to advance primate research and conservation in Myanmar, while following all international funding regulations to Myanmar, despite ongoing government political tensions. Without this, we risk stepping decades back from progress made.
- Strengthening training links with partner academic institutions in the region with strong primatology programs and degrees (e.g., King Mongkut's University of Technology Thonburi (KMUTT) Thailand, National Primate Research Center of Thailand Chulalongkorn University, Universiti Sains Malaysia, Institut Pertanian Bogor University, Indonesia, and Sun Yat-Sen University, China).
- More key academic textbooks translated into the Myanmar language: in the absence of formally translated academic books, an
 informal online forum could help connect primate experts in Myanmar with each other and with the wider scientific and conservation communities around the world.
- Encouragement of international researchers to publish in open access journals to enable primate habitat researchers to access contemporary literature more easily.

4.2. Strategies for multi-stakeholder conservation efforts incorporating government, local and international NGOs to work on joint projects

Sharing experiences from other countries is critical to understanding what works and what does not work for primate conservation and can allow local experts to get ideas about what would be most effective in Myanmar. Methods for information sharing and exchange on real-world implementation include:

- The new IUCN Global Register of Competences for Threatened Species Recovery Practitioners: https://www.iucn.org/commissions/species-survival-commission/resources/a-global-register-competences-threatened-species-recovery-practitioners
- Evaluating other successful multi-stakeholder conservation efforts in neighbouring countries.
- Translations of key documents into the Myanmar language including IUCN Best Practice Guidelines and PA and species action plans from China, Thailand and India.

4.3. Expanding career opportunities for primatologists in Myanmar

Promoting primatology as a valid and sustainable career is one way to encourage young researchers and conservationists to pursue this avenue and to stick with this choice. Much of the career development in Myanmar can, and should be, driven by the academics and

experts in Myanmar, with foreigners who have experience working in Myanmar helping to leverage collaborations and funding, especially as in-country scholarships and grants to study primates do not exist. Some specific ideas for expanding career opportunities for primatologists are:

- Although anthropology departments exist, primatology degrees and modules are unavailable, largely due to the lack of specialised primatology teaching knowledge and the perception that a narrow focus could limit job opportunities. Therefore, an emphasis on supporting long-term national positions for primatologists within anthropology and zoology departments within the Myanmar academic system and Nature and Wildlife Conservation Division of the Forest Department would be beneficial. In addition, primatology modules should be integrated into broader wildlife conservation and management degrees/courses to allow students to apply their training within a conservation framework.
- Regional NGOs and universities to provide primatology field training opportunities to students and researchers. Although there has
 been no primatology-specific training to date, Myanmar Birds and Nature Society and Biodiversity Conservation Society of Sarawak
 (in collaboration with Mandalay University) have both led successful trainings for bird watching and statistical wildlife analyses,
 respectively.
- Enable and facilitate attendance at international conferences.
- Establish a Myanmar Primate Society, to share funding opportunities and to strengthen local capacity to develop proposals.
- Create stronger links with the IUCN Primate Specialist Group and associated sections (e.g., Section on Small Apes (SSA)) to facilitate training access and promotion of career options.

4.4. International recognition of Myanmar national primate research and status reports

Much of the data generated in Myanmar relating to wildlife, and primate conservation in particular, does not make it to international forums. The following suggestions are intended to address this, and would be relatively cost-effective for donors or other supporting organisations:

- Ensure that primatologists from Myanmar are included in contributing to IUCN Red List assessments.
- Assist Myanmar researchers in publishing findings in international primatology journals so that they reach a wider audience (e.g., International Journal of Primatology, American Journal of Primatology, Primates, and Folia Primatologica).
- Funding agencies should require the recipient(s) of their monetary award to publish their work in international open access journals (for which funders would pay through the grant) as opposed to only submitting reports.
- Encourage senior primatologists to not only apply to be members of the IUCN Primate Specialist Group (http://www.primate-sg. org/) or the local Asia Section or species-specific sections (e.g., Section on Small Apes: https://gibbons.asia/) but be given active roles within the working groups.

5. Equity in primate conservation in Myanmar

The "colonization" of conservation activities in developing countries is an important concern and has recently garnered great recognition (Bezanson et al., 2022). Primatologists from Myanmar should be supported to make decisions in Myanmar about primates, and to ensure that any collaboration with international experts is equal and collegiate. Several of the recommendations above directly address some of the systemic challenges that have created the current state of primatology in Myanmar (as in other countries) where the balance between foreign and national scientist gain is not equal (Waters et al., 2021). We make the following suggestions:

- Convene workshops to address concerns from experts in Myanmar, and to develop a positive way forward for national and international collaboration and/or through being adopted as a mandate for all primatology societies. When done appropriately, collaborations can bring in additional funding and expertise to enhance national efforts, whilst supporting Myanmar researchers to pave the way.
- Myanmar researchers could and should agree or adopt an existing code of conduct for ethical research collaboration, requiring
 international researchers to follow human and animal ethical standards in research design and publication of findings, and donors
 should require evidence that research partnerships are equal and fair, and include a specific capacity building aim.
- Where possible, funders could be responsible for ensuring partnerships between international and national NGOs/universities when expertise already exists within Myanmar.
- Lastly, grant applications and journals should be accessible to researchers for whom English is not their first language (e.g., support from journals and grants to help proof-read). Applications and manuscripts should not be being rejected solely based on the quality of the English if the underlying proposal/manuscript is of good scientific quality.

5.1. Species focus for future research

We have highlighted that all Myanmar's primates have significant knowledge gaps and require conservation attention. It is therefore a challenge to highlight species to focus on without more evidence of their plight. However, based on the findings from the systematic literature review, coupled with IUCN Red List statuses and insufficient knowledge on population dynamics, we recommend

focusing on the langur species (notably Phayre's, Shan State, dusky, Indochinese gray and Shortridge's langurs) and Skywalker and lar gibbons. Compared to other primates in Myanmar, all these species are Endangered on the IUCN Red List with unknown population and distribution statuses (Table 1). In addition, the threats to Shan State langurs are also unknown.

6. Conclusion

In summary, we highlight the need to improve the breadth, depth, quality and accessibility of primatological research in Myanmar to conserve some of the world's most threatened primate species. Myanmar's history creates some challenges to achieving this, but nothing that cannot be overcome by a generation of scientists determined to set the stage for the future of primate research and evidence-based conservation action in their country. We have outlined possible steps to support national researchers, from undergraduate and early-career professionals to established primatologists and primate conservation practitioners, to ensure they have the tools to showcase Myanmar as a critical stronghold for primatology research and conservation. The authors and their affiliate organizations stand ready to help implement these suggestions.

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CRediT authorship contribution statement

Carolyn Thompson: Conceptualization, Methodology, Investigation, Writing – original draft, Project administration, Funding acquisition, Writing – review & editing. Ngwe Lwin: Investigation, Writing – original draft, Visualization, Writing – review & editing. Pyae Phyo Aung: Methodology, Investigation, Writing – original draft, Writing – review & editing. Tin Htun Aung: Methodology, Investigation, Writing – original draft, Writing – review & editing. Thura Soe Min Htike: Writing – review & editing. Naw May Lay Thant: Writing – review & editing. Aye Mi San: Writing – review & editing. Christian Roos: Writing – review & editing. Peng-Fei Fan: Writing – review & editing. Writing – review & editing. Mark Grindley: Writing – review & editing. Phyu Pyar Tin: Methodology. No No Wai: Methodology; Htoo Htoo Aung Lwin: Investigation. Kirsten Gilardi: Writing – review & editing. Frank Momberg: Writing – review & editing. Susan M. Cheyne: Methodology, Writing – original draft, Project administration, Funding acquisition, Writing – review & editing. Tierra Smiley Evans: Conceptualization, Methodology, Writing – original draft, Supervision, Project administration, Funding acquisition, Writing – review & editing. Treview & editing. Project administration, Funding acquisition, Writing – review & editing. Project administration, Funding acquisition, Writing – review & editing. Project administration, Funding acquisition, Writing – review & editing.

Declaration of Competing Interest

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Data Availability

Data is available in the Supplementary Files.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02662.

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