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REVIEW OF THE IMPACT AND MITIGATION OF TRANSPORTATION AND SERVICE CORRIDORS ON PRIMATES

ABSTRACT

Most primate populations are declining, with 60% of species facing extinction. The expansion of transportation and service corridors (T&S), i.e. roads, rail, and utility and service lines, poses a significant yet underappreciated threat. With the development of T&S corridors predicted to increase across primates' ranges, it is necessary to understand the current extent of its impacts on primates, the available options to mitigate these effectively, and recognize research and knowledge gaps. By employing a systematic search approach to identify literature that described the relationship between primates and T&S corridors, we extracted information from 327 studies published between 1980 to 2020. Our results revealed that 218 species and subspecies across 62 genera are affected, significantly more than the 92 listed by the IUCN Red List of Threatened Species. The majority of studies took place in Asia (45%), followed by mainland Africa (31%), the Neotropics (22%), and Madagascar (2%). Brazil, Indonesia, Equatorial Guinea, Vietnam, and Madagascar contained the greatest number of affected primate species. Asia featured the highest number of species affected by roads, electrical transmission lines, and pipelines and the only studies addressing the impact of rail and aerial tramways on primates. The impact of seismic lines only emerged in literature from Africa and the Neotropics. Impacts are diverse and multifaceted, e.g. animal-vehicle collisions, electrocutions, habitat loss and fragmentation, impeded movement and genetic exchange, behavioural changes, exposure to pollution, and mortality associated with hunting. Although several mitigation measures were recommended, only 41% of studies focused on their implementation, whilst only 29% evaluated their effectiveness. Finally, there was a clear bias in the species and regions benefiting from research on this topic. We recommend that

government and conservation bodies recognise T&S corridors as a serious and mounting threat to primates and that further research in this area is encouraged.

INTRODUCTION

Human activities and the infrastructure facilitating them greatly impact biodiversity. Whilst some species are able to adapt to human-induced changes, most are unable to and as a result are significantly affected (Alroy 2017). Nonhuman primates (hereafter primates) are one of the groups most affected by human activities (Carvahlo et al. 2019). The majority (75%) of primate species worldwide are currently experiencing considerable population declines (Estrada et al. 2017). Primates are pivotal to many ecosystems and human communities, serving key ecological functions such as seed dispersal and/or pollination, generating income and/or food for people and/or holding cultural significance, whilst also yielding invaluable insights into human evolution (Heymann 2011; Kirkby et al. 2011; van Vliet & Mbazza 2011; Scally et al. 2012; Humle & Hill 2016; Andersen et al. 2018). However, deforestation, hunting, disease, and climate change threaten their existence (Estrada et al. 2017).

Amongst these threats, linear infrastructure, namely roads, rail, electrical transmission lines, gas-oil-water pipelines, seismic lines, and aerial tramways, collectively termed "transportation and service (T&S) corridors", are classified by the International Union for Conservation of Nature (IUCN) as significant contributors to the decline of primates. At present, from a total of 493 extant primate species, the IUCN Red List of Threatened Species (updated 09/07/2020) catalogues 92 (19%) as threatened by T&S corridors, 14 of which are listed as Critically Endangered (IUCN 2020a). T&S corridors are vital for the socio-economic development of many communities and nations; they create and ease access to resources, markets, and work opportunities (Amador-Jimenez & Willis 2012). This results in an increased demand for their expansion in areas where a large proportion of primates occur and where governance and institutional regulations happen to weak (Dulac 2013; Laurance et al. 2014; Berg et al. 2015; Estrada et al. 2018).

The impact of T&S corridors on different taxa is relatively well documented (e.g. van der Ree et al. 2011; Barrientos & Borda-de-Água 2017; Richardson et al. 2017). The causes of wildlife population declines as a result of T&S corridors range from direct mortality to behavioural changes (e.g. Shannon et al. 2014; Sadleir & Linklater 2015). Infrastructure networks transform landscapes, influencing dispersal or migration patterns, food patch availability, and genetic exchange between populations (Strasburg 2006; Goosem 2007). They also facilitate access to activities that further enhance defaunation or deforestation, including hunting, logging, and agriculture (Laurance et al. 2017). Measures to mitigate these impacts are similarly varied, catering to the specific needs of different taxa and assisting movement across habitat fragments, though their effectiveness differs (Rytwinski et al. 2016).

The number of studies assessing the general impact of T&S corridors across different environments has increased steadily in recent years (Richardson et al. 2017; Ghent 2018; Oddone Aquino & Nkomo 2021). Nevertheless, the impact and mitigation of T&S on primates has not yet been thoroughly investigated, nor has it received sufficient attention (Hetman et al. 2019). The majority of studies are scattered, focusing on individual species and single cases (e.g. Cibot et al. 2015; Al-Razi et al. 2019) or fail to address species-specific influences. Consequently, the extent of such impacts on primates remains to be assessed, and the most effective mitigation approaches required to address these impacts still need to be identified (Phalan et al. 2017).

We present here, the first comprehensive systematic review of the impact of T&S corridors on primates. The purpose of this study was to 1) assess the extent and diversity of impacts that T&S corridors have on primates across their ranges. For example, the number and distribution of affected species, the types of T&S corridors affecting different species, the degree of impact, and species' responses to such impacts; 2) understand what mitigation measures have been recommended, implemented, and evaluated – and which have been effective and why?; and 3) highlight gaps in knowledge relating to impacts and mitigation measures, whilst drawing attention to taxonomic and geographical biases in current research.

METHODS

LITERATURE REVIEW PROCESS

We searched for both peer-reviewed and grey literature that described, either directly or indirectly, any form of relationship between primates and T&S corridors. Literature searches were conducted in June 2020 in ISI Web of Science database, Scopus, ProQuest Dissertations and Theses database, and Google Scholar (first 2000 hits). In addition, the bibliography of *State of the Apes: Infrastructure Development and Ape Conservation* (2018) was examined for further relevant literature. We referred to the IUCN Red List to ensure that every primate group threatened by T&S corridors was included in our keyword search string. In addition, the terms "ape", "monkey", and "primate" were used to expand the search results and include potential studies related to species left off the IUCN's list. Altogether, the keyword string used was as follows: ("gorilla*", "chimpanzee*", "orangutan*", "gibbon*", "loris*", "macaque*", "langur*", "snub-nosed monkey*", "mangabey*", "colobus*", "mandrill*", "drill*", "guenon*", "galago*", "lemur*", "sifaka*", "indri*", "aye-aye*", "tamarin*", "titi*", "night monkey*", "spider monkey*", "howler*", "capuchin*", "woolly*", "saki*", "marmoset*", "squirrel monkey*", "ape*", "monkey*", OR "primate*") AND ("road*", "highway*", "roadkill*", "rail*", "electrical transmission*", "electrocution*", "pipeline*", "seismic*", "oil*", OR "tramway*").

Since there has been no previous review relating to this topic, it was necessary to cover a significant volume of relevant literature. In this regard, no restrictions were set for study dates, sample sizes, time frames, and study designs. However, only literature published in the English language was considered. Literature that described or discussed any type of T&S corridor impact on primates, as well as any form of mitigation measure was included. We elected to focus solely on the negative impacts of T&S corridors on primates and thus defined an "impact" as any threat or activity that has affected or may affect the conservation status of a primate taxon. A single observation of a primate hesitating to cross a road was not considered an impact, but the repeated observations of primates failing to travel to an area due to the presence of a road was. We did not explore any positive impacts which T&S corridors may have on primates in this review as our focus was to expand on mitigation measures that counter the negative impacts of T&S corridors and assess their effectiveness.

Only studies presenting empirical evidence were considered. Thus, reviews, self-reports, news articles, and editorials were excluded. Studies were also excluded if they did not mention any specific impacts or mitigation measures to primates, even if they indicated that T&S corridors are affecting habitats within their known range. In this way, no assumptions about any impacts were made without empirical evidence. Finally, we omitted any studies that took place in zoos or laboratory environments, choosing to focus on the impacts of T&S corridors on primates in the wild. Study screening was conducted at the full-text level, rather than only titles and abstracts. This way, we were able increase the level of review robustness by thoroughly analysing the contents of each work of literature to determine relevance and inclusion (see Supporting Information for study flowchart).

DATA EXTRACTION

From each included study, we extracted information about the author/s and publication date, type of literature, study design, study continent, country, location, specific site (if available), protection status of location, geographical location (latitude and longitude, decimal degrees), species or subspecies studied (common name, Latin binomial, family, IUCN conservation status), types of T&S corridors affecting species studied, impacts (divided into "direct" and "indirect"), summary-of-findings/quotes from studies, and mitigation measures (divided into recommended, implemented, and evaluated). Based on the definition found in *State of the Apes Volume lll: Infrastructure Development and Ape Conservation* (pp. 42), we classified "direct impacts" as those impacts which primates may be immediately faced with during and after the development of T&S corridors (e.g. death, injury, habitat loss, barriers). On the other hand, we considered "indirect impacts" to be those impacts which come about as a collateral effect of the direct impacts (e.g. habitat loss opens up areas to human activities and the introduction of disease). If mitigation measures were implemented in a study, based on the information provided, they were categorised as either "effective", "partially effective", "not effective", or "not evaluated". In this case, an "effective" mitigation measure is one that significantly diminished or virtually eliminated a threat faced by all primate species in a given area. For a mitigation measure to be considered "partially effective", a threat would only be slightly diminished and/or not benefit all primate species in a given area. We considered publications from the same sites independently when assessing the number of studies that have taken place. However, these were then pooled and considered as a single data unit when analysing impacts and mitigation measures. Subspecies were also included in the data extraction process, under the assumption that subspecies in different locations may be affected differently, and thus may require their own unique management interventions.

DATA ANALYSES

The extracted data were filtered by geographical region and primate family to generate results in the form of maps, tables, charts, and diagrams pertaining to the objectives of this review. Since the data were not normally distributed, we used Spearman's Correlation Coefficient to test the relationship between primate species richness per country and the number of identified studies related to primates and T&S corridors per country. Statistical significance was set at $p<0.05$.

RESULTS

Out of 523 studies, 327 were identified as suitable and included in this review. Since 1980, there was a 21-fold increase in the number of studies related to the impact of T&S corridors on primates. The last five years witnessed a peak in relevant studies (Fig. 1). The majority of studies were conducted in Asia (45%), followed by mainland Africa (31%), the Neotropics (22%), and Madagascar (2%). There was a significant positive correlation between country-level primate species' richness and the number of studies identified for each country (Spearman rank correlation: R_s=0.415; N=90, $p < 0.001$). The greatest number of studies took place in India, China, and Brazil. However, albeit the high number of primate species found on Madagascar (22% of all primate species globally), very few studies from this primate-rich country focused on primates and T&S corridors (Fig. 2). Several countries home to primate species, especially in mainland Africa, have not yet had any T&S corridor-related studies conducted within them, emphasising the overall lack of research in this area. While most of the locations studied were within protected areas (44%), 35% were within partially-protected areas, i.e. study locations that straddle protected area delimitation (see Supporting Information).

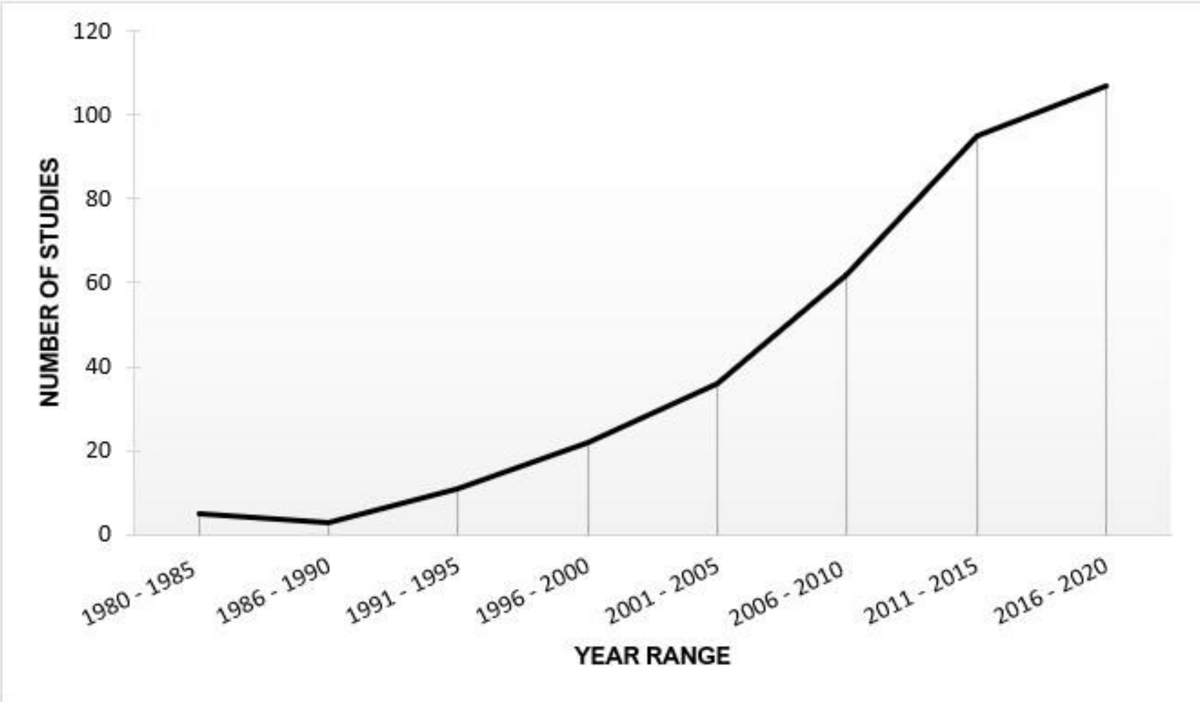

Figure 1. The number of studies related to the impact of transportation and service corridors on primates published between 1980 and 2020.

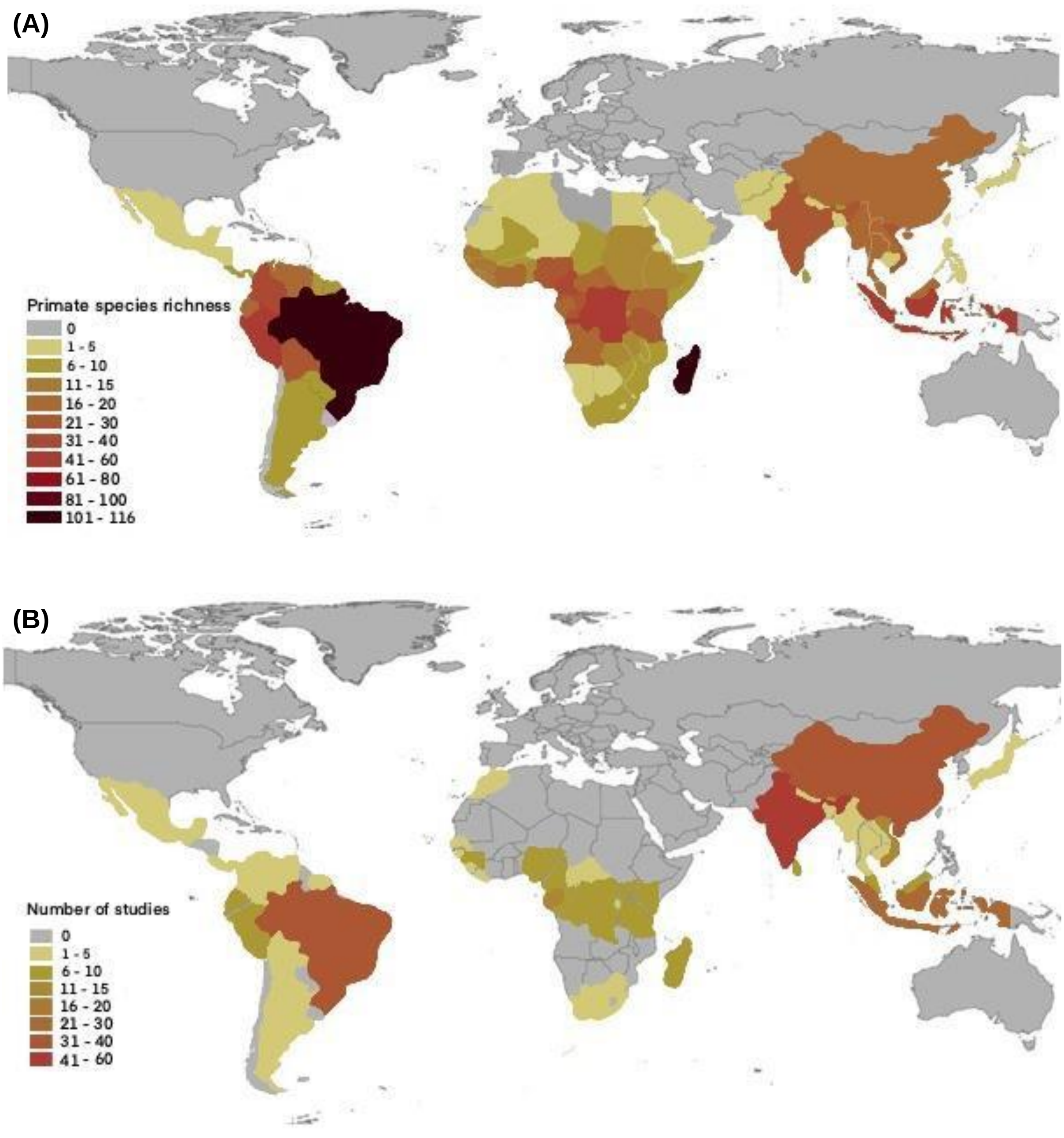

Figure 2. (**A)** The number of primate species per country across Asia, mainland Africa, Madagascar, and the Neotropics (IUCN 2020b). **(B)** The number of studies per country related to the impact of transportation and service corridors on primates.

The number of primate species and subspecies affected by T&S corridors as reported in the literature was significantly higher than that catalogued by the IUCN Red List. Compared to the 92 species (including 9 subspecies) listed by the IUCN, this study found a total of 218 species and subspecies to be affected (Fig. 3). Nevertheless, the search process failed to identify any studies for 21 species listed by the IUCN as threatened by T&S corridors (see Supporting Information). We found Brazil to report the highest number of primate species affected by T&S corridors, followed by Indonesia, Equatorial Guinea, Vietnam, and Madagascar (Fig. 4). The number of studies per primate genus differed considerably. Genera that contained a high number of species did not necessarily report the greatest number of studies. Indeed, some genera containing fewer species (particularly among great apes) revealed a disproportionately greater number of studies (Fig. 5).

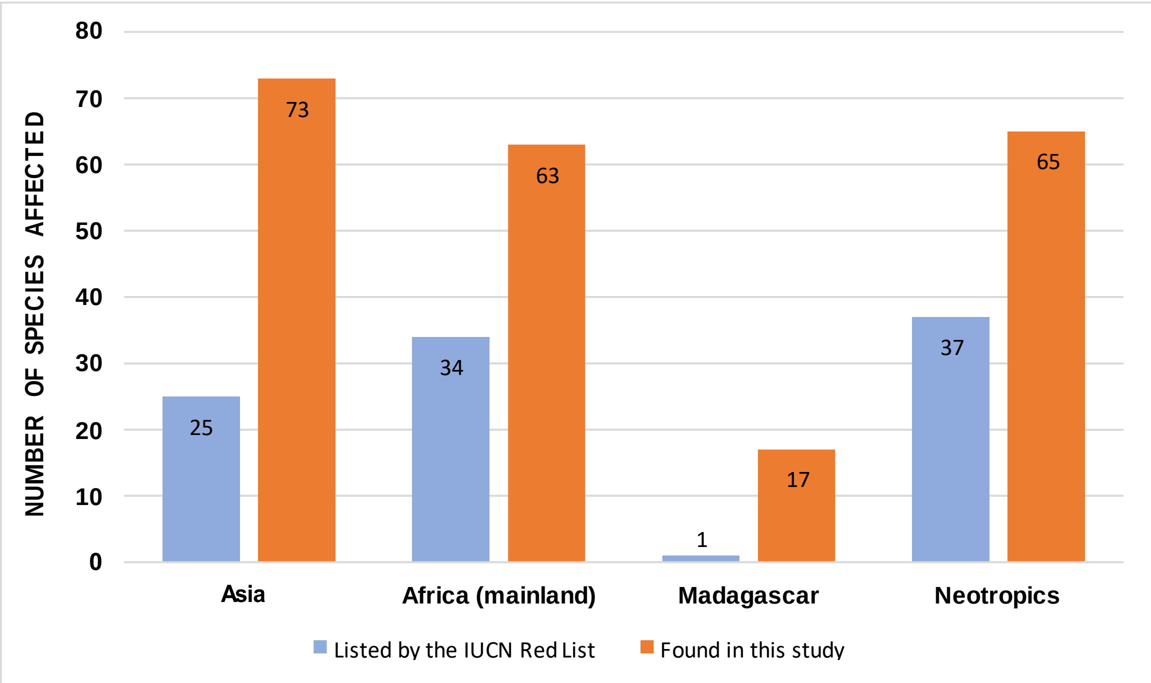

Figure 3. A comparison of the number of primate species and subspecies affected by transportation and service corridors as listed by the IUCN Red List of Threatened Species and the number identified in this study.

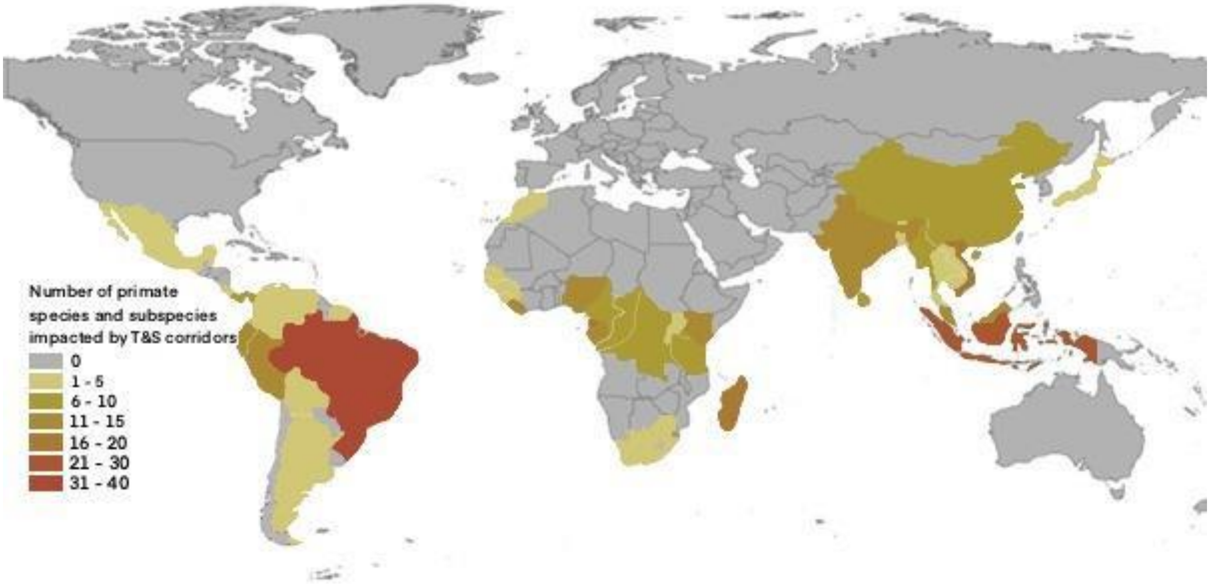

Figure 4. The geographic distribution of the number of primate species and subspecies affected by transportation and service corridors based on the reviewed literature identified as relevant in this study.

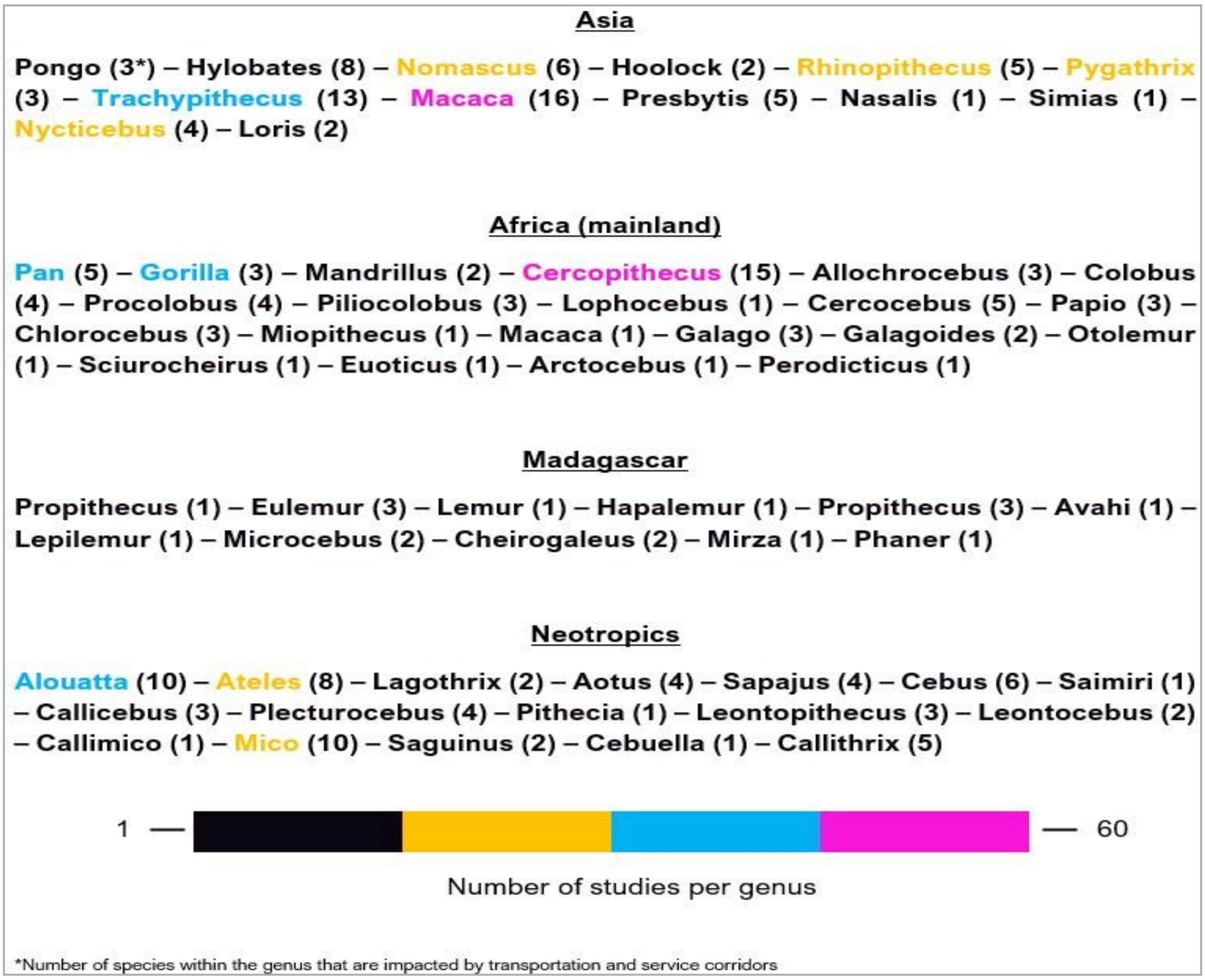

Figure 5. The genera of all primate species affected by transportation and service corridors by region. The numbers within the parentheses beside the genera represent the number of species and subspecies within that genus that

are reported in the literature to be affected by transportation and service corridors. The number of studies each genera were the subject are colour coded as per the legend in the figure.

We found roads to affect nearly all primate species identified in this review. In fact, roads were the only type of T&S corridor reported to affect primates in Madagascar. Within the literature we identified, Asia featured the highest number of species affected by roads, electrical transmission lines, and pipelines, whilst being the only region reporting studies on the impact of rail and aerial tramways. Reports of the impact of seismic lines were only reported amongst primates in Africa and one species in the Neotropics (Fig. 6).

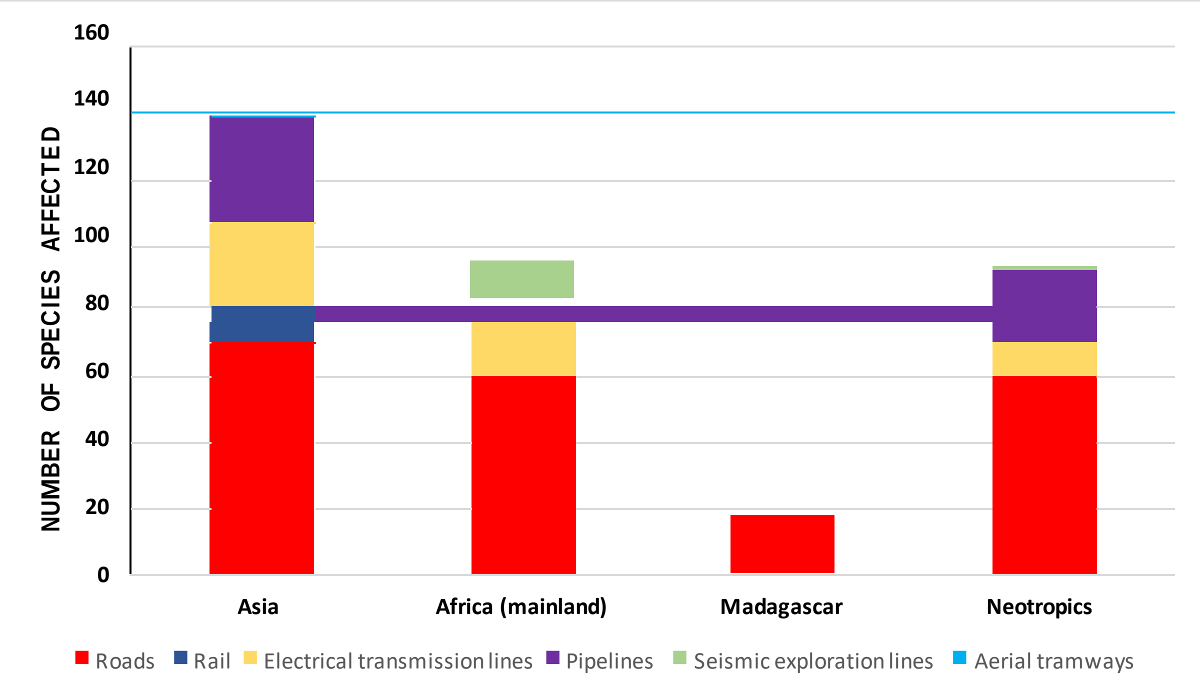

Figure 6. The different types of transportation and service corridors and the number of primate species they impact across their ranges, based on reviewed literature.

The specific impacts of T&S corridors on primates varied greatly, with 21 different impacts listed (12 direct impacts and 8 indirect impacts). The greatest impacts on all species were habitat loss and fragmentation, death or injury, and human activities (Fig. 7) (see Supporting Information for a complete list of the primate species found to be affected by T&S corridors, the type of corridors affecting them, as well as the specific impacts on each species). Asian and Neotropical primates were found to experience "direct impacts" most frequently (Fig. 7).

We found no appreciable difference between the percentage of at-risk primates (Near Threatened, Vulnerable, Endangered, Critically Endangered) and lower risk primates (Least Concern, Data Deficient) facing these specific impacts, regardless of their habitat region (see Supporting Information).

The mitigation measures identified in this review were considerably diverse. We divided them into "direct interventions" and "measures aimed at modifying or managing human behaviours". Ultimately, 10 main mitigation measures emerged (Fig. 8). Of the mitigation measures we classified as direct interventions, the installation of wildlife crossing structures and the avoidance of further infrastructure development within forests were most frequently recommended. Of the measures aimed at changing human behaviours, educating users of T&S corridors and regulating anthropogenic processes within forests were suggested most frequently. Although many mitigation measures were recommended, few were implemented (41% of studies), whilst only 29% of the total studies evaluated these for their effectiveness (Fig. 8). Of the 96 studies that evaluated the effectiveness of implemented mitigation measures, nearly all of them (94 studies) concluded that the measures in place were either effective or partially effective. Wildlife crossings were the most frequently implemented (43% of studies) and evaluated mitigation measure (75% of studies that implemented them were evaluated). Translocations were not evaluated for effectiveness by any study identified in this review. Furthermore, fencing was the only mitigation measure that was not implemented (and thus neither evaluated) (Fig. 8).

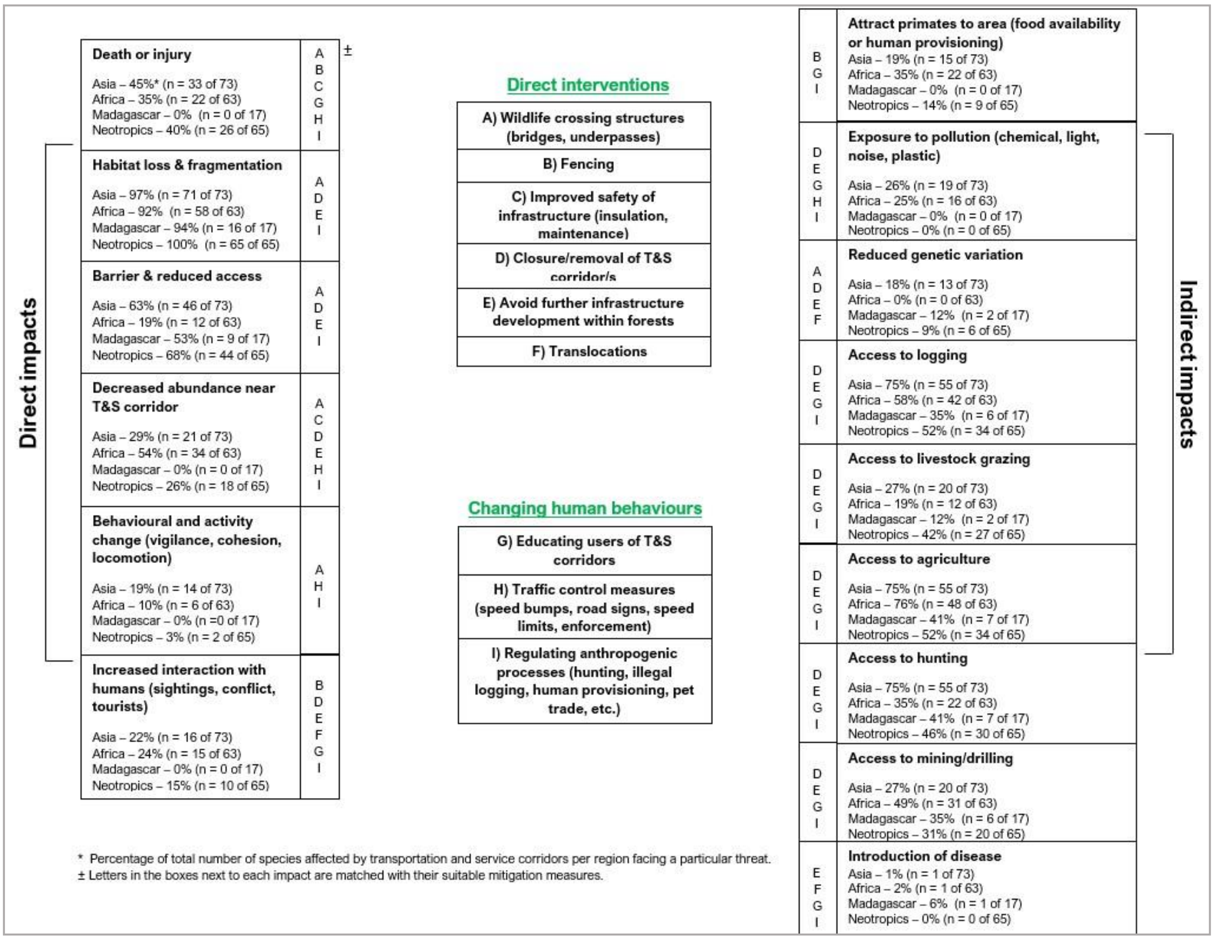

Figure 7. The impacts of transportation and service corridors on primates, divided into direct and indirect impacts. For each impact, we report the percentage of species affected (from the total number of affected species) within each region. The boxes in the centre represent all the mitigation measures identified during the course of this review, divided into direct interventions and measures aimed at changing human behaviour. The letters beside each impact correspond with the associated mitigation measures that were implemented or suggested within the literature.

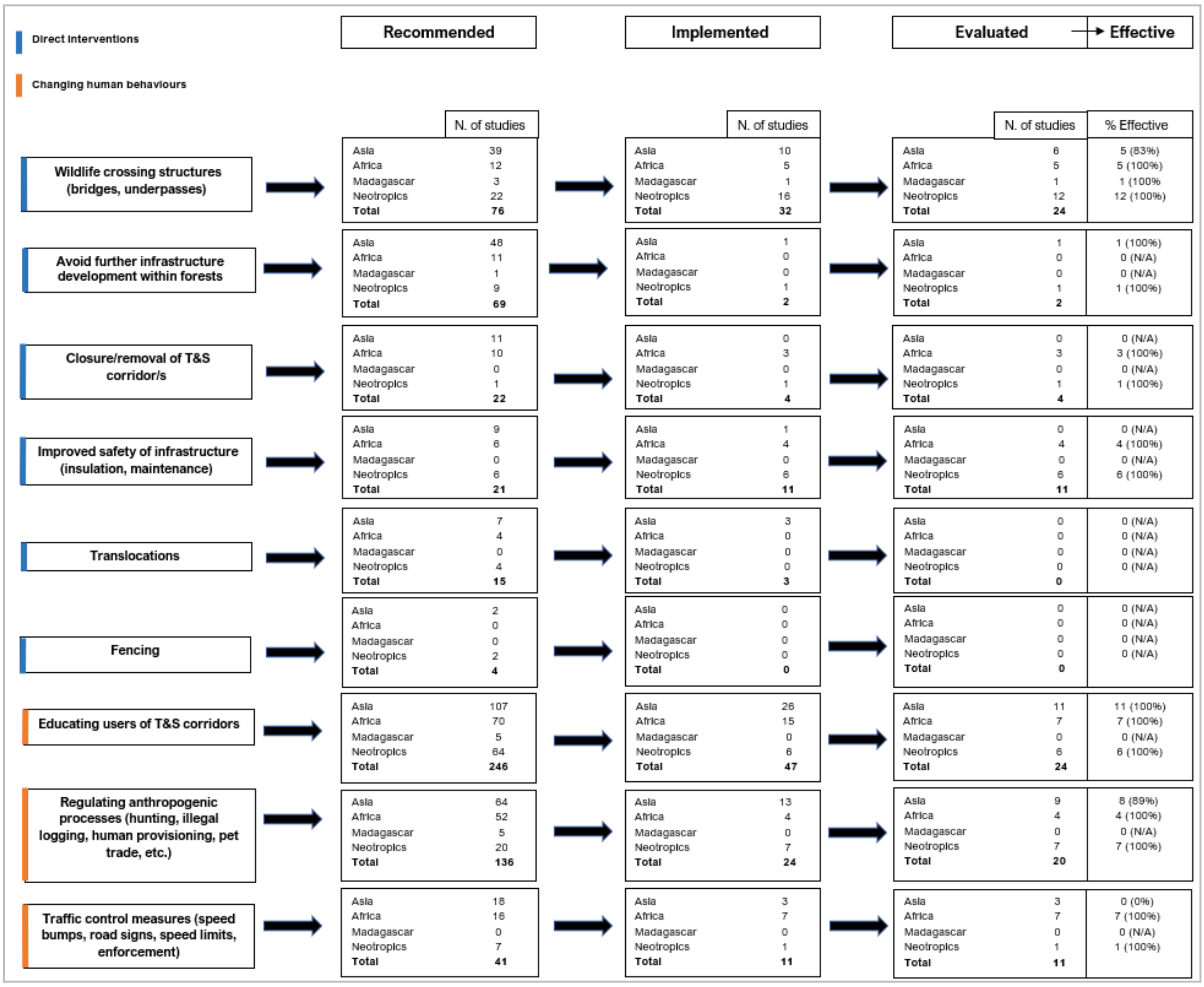

Figure 8. All mitigation measures for the impact of transportation and service corridors on primates identified during this review (blue = direct interventions, orange = changing human behaviours). For each mitigation measure, we have listed the number of studies per region that recommended it, implemented it, and evaluated its effectiveness. If mitigation measures were evaluated, the final column provides the number and percentage of evaluated studies that regarded them as effective or partially effective.

DISCUSSION

THE IMPACT OF T&S CORRIDORS ON PRIMATES

Primates across all four regions where they occur, i.e. Asia, mainland Africa, Madagascar, and the Neotropics, were found to be affected by at least one type of T&S corridor. Roads were the corridor type with the greatest and most widespread impact on primates. Roads are rapidly expanding into areas that have until now been relatively road-free. Laurance et al. (2014) projected that there will be a 60% increase in the total length of roads by the year 2050 compared with 2010, i.e. an additional 25 million kilometres. The impacts from roads affected all primate families and at least one species from each genera. Deaths or injury as a result of road collisions were most commonly reported in primates within the Cercopithecidae (both Asia and Africa) and Atelidae families. Cercopithecidae in Asia, which includes predominantly semi-terrestrial species, are frequently involved in road collisions after being attracted to roads by the food availability at roadsides and provisioning from humans, be it for cultural reasons (Sharma 2013) or tourism (Wong et al. 1999). In the Neotropics, canopy discontinuity caused by road construction may force commonly arboreal species to descend to the ground and attempt to cross, leading to potential collisions (Pozo-Montuy et al 2011). Though road collisions do occur in Africa (see Supporting Information), the greater number of unpaved roads may have resulted in the lower rates of reported collisions. This may also reflect a potential research bias. Nevertheless, the projected paving of roads throughout Africa could increase the frequency of future collisions (Ngezahayo et al. 2019).

Vehicles in Africa do, however, collide with chimpanzees, affecting the dynamics of social groups (Cibot et al. 2015; Krief et al. 2020). In contrast, we found no reported road collisions for great and small apes in Asia, i.e. orang-utans and gibbons. Perhaps because gibbons are highly arboreal, loss of canopy connectivity linked to roads often represents extreme barriers to their movement (Alamgir et al 2019). Although orang-utans are similarly arboreal, they also possess the capacity for terrestrial locomotion especially in disturbed habitats (Ancrenaz et al. 2014). Their ability to cross open landscapes may mean they are better suited to cope with fragmentation caused by T&S corridors, but it also increases their susceptibility to vehicle collisions, hunting, and capture for the pet trade. Literature from Madagascar was also void of reports of road collisions, although the reason for this could be linked to a lack of empirical research and/or inclusion of cases in publications. Many more primates species and subspecies (N=60) suffered mortality by road collisions than is reported in the IUCN Red List as threatened by T&S corridors. Moreover, 14 of these species and subspecies that were not listed by the IUCN Red List as threatened by T&S corridors were either Endangered or Critically Endangered (e.g. Inogwabini & Thompson 2013; Ferreguetti et al. 2020) (see Supporting Information for complete list). These findings suggest that a revision of the threats listings is potentially needed so that the impact of T&S corridors is more accurately captured on the IUCN Red List assessments for individual species and subspecies. This is especially important given the Red List's major influence on conservation outcomes (Betts et al. 2020). Regardless of whether collisions occur or not, roads penetrating through primates' habitats have the capacity to alter individual and group behaviour, increasing vigilance, and enhancing or disrupting social cohesion (Hockings et al. 2006; Moor et al 2019). Furthermore, primates perceiving roads and the activities they facilitate as a risk may actively avoid frequenting and using such areas (Morgan et al. 2019).

The most widespread impacts on primates from road infrastructure included habitat loss and fragmentation. These can result in secondary direct and indirect impacts, including a reduction in access to resources and hence primates' abundance near roads, and in genetic exchange between populations (Li et al., 2015; Aquino et al. 2016). Roads open up previously undisturbed areas to numerous anthropogenic activities, namely logging, hunting, agriculture, livestock grazing, and mining/drilling (e.g. Rawson et al. 2011). In many cases, these activities occur in unison, significantly impacting the entire landscape (e.g. Xiang et al 2009). Legally authorised roads created for improved settlement connection, access to industrial operations (logging, oil concessions, mining), or tourism purposes are generally wide and high in traffic volume (Rogers & Hennessey 2008). These tend to encourage new settlements and increase access to and establishment of bushmeat markets along roadsides, which enhances hunting pressures on primates (Franzen 2006). Legally-authorised roads may also give rise to the creation of unauthorised secondary roads created by both locals and industrial workers for hunting, capturing wildlife for the pet trade, logging, and artisanal mining (Ulibarri & Streicher 2012; Boyer Ontl 2017). Apart from the more obvious impacts of increased access generated by roads, vehicle traffic and industrial activities may also affect primates either through noise, light, atmospheric pollutants, or dumping of plastic waste along roadsides (e.g. Cibot et al. 2015; Duarte et al. 2018).

After roads, electrical transmission lines and pipelines were identified as the T&S corridors posing the greatest threat towards primates. Similar to roads, these corridors are strongly associated with deforestation in primate habitats as a consequence of their construction processes (e.g. Tielen 2016; Costa-Araújo et al. 2019; Thinley et al. 2020). Arboreal and semi-terrestrial primates that would normally use tree branches to brachiate or cross between canopies are at a risk of death by electrocution from exposed transmission lines (e.g. Moore et al. 2010; Chetry et al. 2010; Rodriguez & Martinez, 2014). This is especially the case for primates that have adapted well to anthropogenic environments outside of protected areas, such as howler monkeys (genus *Alouatta*) and colobus monkeys (genus *Colobus*), and hence make frequent use of human infrastructure (Lokschin et al. 2009; Cunneyworth & Duke 2020). Pipelines associated with hydroelectric, gas, and oil projects severely fragment primate habitats (e.g. Thurber et al. 2005; Wich et al. 2019). They also require the creation of additional access roads for construction and maintenance, potentially boosting other activities such as logging and hunting (Laurance et al. 2006). The impacts of pipelines are similar to those of seismic lines. We found seismic lines to reportedly impact primates only in Africa and one Neotropical species, and such lines resulted in typically extensive habitat loss and increased access to human activities (Wallace et al. 2006; Ikapi 2016).

In Asia, railway tracks were found to cause habitat loss and fragmentation in a similar manner to roads. However, despite presenting an extreme barrier to highly arboreal primates, literature suggests they act less as a barrier to semi-terrestrial primates than roads and caused less collisions, potentially because of lower and more predictable rail traffic volume (Sharma, 2009). Aerial tramways were only reported to impact grey snub-nosed monkeys (*Rhinopithecus brelichi*) in Fanjingshan National Nature Reserve, China. The aerial tramway for tourists has fragmented their habitat, permanently blocking their southward movement to areas which they used to frequent in the past (Yanqing et al. 2009).

MITIGATION MEASURES

Mitigating the impact of T&S corridors on biodiversity requires a two-fold approach: the first being *in situ* interventions that reduce impacts directly on-site, the second being measures taken before infrastructure is developed and educating users of T&S corridors once development is complete (Hedlund et al. 2004). Direct interventions to reduce roadkill and facilitate movement across fragments are diverse and must consider whether animals are preferentially terrestrial or arboreal. Across Europe and North America, large, engineered bridges and underpasses constructed over or under roads, railroads, and other T&S corridors are widespread and in most cases highly effective (Clevenger & Huijser 2012; Beben 2016). Wildlife crossings suspended between trees and other structures for arboreal animals have also been used extensively with significant success (e.g. Soanes et al. 2017).

We found numerous wildlife crossing structures that effectively aid primate travel between fragments created by T&S corridors or activities that have been facilitated by T&S corridors. These structures can be of minimal cost to construct and maintain. Yap and Ruppert (2019) installed Malaysia's first urban canopy bridge made from upcycled firehose in Penang to successfully aid the crossing of dusky langurs (*Trachypithecus obscurus*) and long-tailed macaques (*Macaca fascicularis*). A camera trap monitors the use of the canopy bridge. In 2020, this bridge was reinforced with a second prototype design using a double twisted liana with ladders and a solar panel to charge the camera trap (J. Yap, pers. communication). In Borajan, India, bamboo poles allow western hoolock gibbons (*Hoolock hoolock*) to travel with their natural locomotion, i.e. brachiation, over a heavily grazed landscape. This and other crossings can be included in ecotourism programmes if placed in strategic locations (Das et al. 2009). Waterline bridges in Cipaganti, West Java, are effectively used to facilitate movement

of Javan slow lorises (*Nycticebus javanicus*) across agriculture landscapes whilst simultaneously irrigating crops of local farmers who in turn maintain the bridges (Birot et al.
319 2019).

The "colobridges" along Diani beach, Kenya, have successfully mitigated roadkill and electrocutions of Angola black-and-white colobuses (*Colobus angolensis palliatus*), Skyes' monkeys (*Cercopithecus albogularis*), Hilgert's vervet monkeys (*Chlorocebus pygerythrus hilgerti*), and white-tailed small-eared galagos (*Otolemur garnettii lasiotis*) over a busy road frequented by tourists. By 2013, 28 bridges had been erected in areas known to be hotspots for mortality along the 10km stretch of road. Primates still, however, occasionally descend to the ground to cross roads at times (Cunneyworth & Duke 2020). In the Limpopo Province of South Africa, canopy overpasses were installed for guenons (Cercopithecidae) over farm roads. Pole bridges were much preferred over a rope ladder design. The bridges were also preferred by all age-sex classes of guenons over trees and the ground when the tree canopy was open (Linden et al. 2020). In Madagascar, two types of "lemur bridge" designs were reported to effectively allow movement across roads. A suspension bridge design was used more frequently than a plank bridge design, though it took nearly a year from their establishment before lemurs began to use them regularly because of the time needed to habituate to these novel structures (Mass et al. 2011).

Large bridges and underpasses similar to ones in Europe and North America were not recommended for great apes in Africa, as they are a significant expense and there is no guarantee that they will be used (McLennan & Asiimwe 2016). In India, the Assam Forest Department unsuccessfully attempted to establish overpasses across a railway track for western hoolock gibbons (*Hoolock hoolock*) (Sharma 2009). Two steel ropes (wrapped in green plastic cover) were put in place in Hollongapar Gibbon Sanctuary, India, but it did not work. The steel ropes may have been too artificial a lure for the gibbons (Sharma 2009).

Canopy bridges built throughout forests and urban areas in Brazil, Peru, Mexico, Ecuador, and Costa Rica feature a diversity of structural designs. Here, Neotropical primates are distinct from primates in Asia and Africa by generally having much less body weight, less terrestrial adaptation, and prehensile tails for some (Defler 2009). Suiting these unique adaptations, the structural designs of the bridges include horizontal "ship ladders" (Lokschin et al. 2009), nylon rope bridges (Teixeira et al. 2013), semi-artificial bridges using liana (Balbuena et al. 2019), pole bridges (Padua & Padua 1995), and silk rope bridges (Hernández-Pérez 2016), all of which proved to be effective. Thurber et al. (2005) and Gregory et al. (2013) provide detailed protocols and best practices for establishing and monitoring primate arboreal crossings during T&S corridor development processes and after they are complete, advocating that they become necessary inclusions in Environmental Impact Assessments (EIAs). Teixeira et al. (2013) also suggest monitoring outcomes of individual survival, group persistence, population demography, and gene flow of primates once crossings are in place.

Aside from crossings, traffic control measures and insulation of electrical transmission lines have been implemented to prevent primate collisions and electrocutions. Insulation is simple and effective enough, either using insulated lines and terminal bridges when building new transmission towers, upgrading existing ones that are exposed, or braiding multiple lines into one insulated line to reduce the risk of electrocution (Lokschin et al. 2009; Katsis et al. 2018). Effective traffic control measures are slightly more complex to achieve. Options include speed bumps, animal detection-warning systems that either detect animals before they enter the road and warn drivers or detect drivers and warn wildlife with a variety of audio-visual signals, automated speed detectors (interceptors), the use of lighting reflectors at night, and primate-crossing road signage (Huijser et al. 2015; Hatti & Mubeen 2019). Although these measures can be effective at reducing collisions when placed along roads (Cunneyworth & Duke 2020), they do not always work because drivers may neglect these measures due to lack of proper enforcement (Kioko et al 2015).

It is suggested that education and awareness campaigns are needed to complement traffic control measures. Increased awareness of the threats drivers pose towards primates may modify behaviour and change attitudes concerning road collisions (Crawford & Andrews 2016). Together with enforcement and road signs, these campaigns may also help to deter locals and tourists from feeding primates at roadsides, reducing the risk of primates crossing roads and being struck by vehicles (Fuentes et al. 2008). These measures may however not always be successful. For example, campaigns and signs in Pench National Park, India, requesting locals to avoid feeding rhesus macaques (*Macaca mulatta*) at roadsides are generally ignored due to the significance of the monkeys in religious beliefs, which encourages provisioning (Pragatheesh 2011). The connection between wildlife conservation and human socio-cultural contexts can complicate interventions; deliberate efforts to orchestrate value shifts for conservation are rarely effective (McKenzie-Mohr 2013). Rather, a multilevel understanding of values is required to improve the utility of conservation action. This includes coordinating conservation actions involving societies and their institutions, communities, individuals, and organizations. Although conservation professionals may initially struggle to inform deliberate value shifts, they should pursue ways to induce change within society that will facilitate more effective adaptation to social-ecological threats (Manfredo et al. 2016).

The high success rate of the reported mitigation measures that were implemented (98% were deemed effective or partially effective) highlights that when properly executed with necessary follow-up, management systems, and monitoring, various mitigation measures can successfully tackle a variety of impacts (Sánchez & Gallardo 2005). However, it is important to recognise that despite this success rate, ineffective mitigation strategies or case studies may not have been published, which is commonplace in conservation evaluations (Josefsson et al. 2020). This may have generated a bias in our results. Furthermore, despite their relative effectiveness, the majority of these measures can draw attention away from the wider threat faced by primates: the unsustainable expansion of T&S corridors. Addressing this problem requires a concentrated effort between regional government and conservation bodies to review T&S infrastructure projects and their impact on primates before, during, and after development, not fearing the prospect of abandoning projects altogether if necessary and considering less impactful, albeit possibly more expensive, alternatives (Laurence et al. 2020). It is also critical to consider the indirect impacts of new T&S corridors before development begins. Plans should be made to close T&S corridors once industrial operations are complete to block off access and allow reforestation to take place (Brugière & Gautier 1999), whilst investing in strengthening protected area management and relevant laws safeguarding biodiversity (Wilkie et al. 2016; Strindberg et al. 2018).

The only two mitigation measures not evaluated by any study identified in this review were translocations and fencing. The use of translocations as a conservation tool is a contentious issue; they are costly to execute and offer variable results due to the different factors that can determine their success (Sherman et al. 2020; Langridge et al. 2020). In Arunachal Pradesh, India, "a few isolated groups" of eastern hoolock gibbons (*Hoolock leuconedys*) were translocated from unprotected forest fragments disturbed by road construction and permanent human settlement to the Mehao Wildlife Sanctuary, although they have not yet been monitored since (Kumar et al. 2013). In Vietnam's Van Long Nature Reserve, plans to translocate subpopulations of Delacour's langur (*Trachypithecus delacouri*) are currently being explored to combat population structuring in isolated fragments separated by roads (Ebenau et al. 2011). Besides these two studies, most others we identified did not recommend translocations as a mitigation measure, either because of uncertain long-term population viability (Moraes et al. 2018), cost (Struhsaker & Siex 1998), or undesired outcomes (Moore et al. 2014). As for fencing, we found no evidence for the effects of installing barriers to prevent primates from crossing gaps created by T&S corridors. What we know is that fencing designs and materials can be expensive and primates (particularly smaller, agile ones) may bypass them with ease (Strum 1994). If a fencing design proves to be effective, it may impede movement, dispersal, and access to resources (Smith et al. 2020).

RESEARCH GAPS

To protect primates facing the threat of T&S corridors, science has to provide a better platform for government bodies and decision-makers to understand the complex relationship between these types of infrastructure development, humans' livelihoods, and primates. Research can generate concrete evidence of specific impacts, population changes, and threats to the survival of primates. More emphasis should be placed on avoiding the impacts of T&S corridors in the first instance and developing measures to mitigate these impacts in the second instance. If implemented, these measures should be evaluated for effectiveness. Mitigating the threat of T&S corridors is not a straightforward process and requires creativity and collaboration to achieve success and an understanding of the biology and behavioural ecology of individual species. Implementing mitigation measures and evaluating their effectiveness will allow for widespread dissemination of new insights gained and provide clear evidence for greater funding opportunities. Unfortunately, failure to follow-up on mitigation interventions is not an issue solely associated with the findings of this review but is a widespread problem in primate conservation (Junker et al. 2020).

There is considerable bias in the species and regions benefitting from research related to the impact of T&S corridors on primates (Fig. 2 & Fig. 5). Many affected species remain poorly studied and their responses to the complex and multileveled threats of T&S corridors are poorly understood. Moreover, nearly a quarter of the species listed as threatened by T&S corridors have not yet received any research attention. The obstacles to research efforts may be generally attributed to insufficient funding and resources, and a lack of prioritisation (Bachman et al. 2019).

The IUCN Red List's catalogue of primates threatened by T&S corridors requires updating if it is to act as a much-needed platform guiding research and management efforts. We found many more primate species and subspecies affected by T&S corridors than are listed as being threatened by T&S corridors. Experts play an integral role in reviewing the information required to allocate species within IUCN Red List status classifications, and are backed by data, sources, justifications, estimates of uncertainty in data quality, and peer review (Rodrigues et al. 2006). IUCN Red List assessments are also required to provide a range of supporting information, including threats to taxa, before they can be accepted forpublication. In this case, only "major" threats to species are necessary. To decide what constitutes "major" and "minor" threats, their level of impact is calculated using a scoring system that accounts for the "timing of threats (i.e. past, ongoing or future), their scope (i.e. the proportion of the total population affected), and severity (i.e. the overall declines caused by the threat)" (IUCN 2021). "Minor" threats are not required for IUCN Red List assessments, whilst both major and minor threats are not necessary for Least Concern and Data Deficient taxa. The latter may explain why 43 species and subspecies (40 Least Concern and 3 Data Deficient) are not listed as being threatened by T&S corridors. As for the other 73 species with more severe conservation statuses, T&S corridors may not have been considered as a "major" threat to their populations upon assessment, although this may be a result of the lack of available literature or the bias present in species and regions benefitting from research.

RECOMMENDATIONS

This review illustrates how T&S corridors are contributing to the decline of primate populations across their entire global range. The impacts on different primate species are diverse and multifaceted, occurring during corridor development and lasting for many years after completion. The complexity of addressing this threat lies in the fact that whilst many humans are dependent on T&S corridors, they are often established without appropriate EIAs and thus expand unsustainably. Furthermore, gaps in our understanding of the impacts of T&S corridors on many primate species and subspecies across various countries have made it increasingly challenging to implement mitigation measures on a larger scale. If the development of a T&S corridor is deemed necessary after impact assessments are carried out, our review indicates that shifting development away from critical zones that contain physical or biological features essential to primate conservation is advisable. Even if the total length of a T&S corridor's intrusion is increased, ensuring the avoidance of major impacts wherever possible may be more effective in terms of conservation than trying to mitigate for their presence (Al-Razi et al. 2019).

We recommend that apart from expanding research efforts, T&S corridors are also recognised by government and conservation bodies as a mounting threat towards primates and other animals. A clear direction is needed for the management of T&S corridors already in place and the assessment of those being planned. Ideally, primates and other animal groups affected by T&S corridor developments are safeguarded before, during, and after development takes place. Regional governing and funding bodies should ensure that developers and users of T&S corridors are properly regulated, sanctioned, and made aware of the threat which they pose to primates, other biodiversity, and ecosystem integrity.

SUPPORTING INFORMATION

Primate species and subspecies affected by transportation and service corridors (Appendix S1), geographical distribution of studies (Appendix S2), study flowchart (Appendix S3), and literature reviewed (Appendix S4) are available after Literature Cited. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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