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Asian primates in fragments: Understanding causes and consequences of fragmentation, and predicting primate population viability

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Abstract

Ongoing efforts to conserve the Asian primates are severely challenged by increasing rates of habitat loss and fragmentation. Underlying drivers such as rapid economic and population growth throughout much of South, East, and Southeast Asia have confined several populations of Asian primates to isolated fragments. Conservation efforts for these primates are partly hampered by a poor understanding of fragmentation, resulting in an inability to draw up effective long-term conservation responses. In this manuscript, I show that fragmentation can be understood better when treated both as stress and a threat. Moreover, despite a myriad of causes of fragmentation reported, most are broad descriptions or subject to various interpretations. Here I describe the use of the IUCN-CMP Unified Classifications of Direct Threats Version 3.2, a convenient and universal tool, for more precise identification of the causes and consequences of fragmentation for Asian primates. I further describe the interrelated variables influencing the persistence of Asian primates in fragments, and the conditions affecting these variables.

KEYWORDS

Asian primates, fragmentation, influencing variables, IUCN-CMP Unified Classifications of Direct Threats Version 3.2, population viability

1 | INTRODUCTION

Throughout their ranges, primates face a myriad of threats—primarily habitat loss, degradation, and fragmentation, and hunting or trapping (Almeida-Rocha, Peres, & Oliveira, 2017; Boonratana, 2013b; Chapman & Peres, 2001; Cowlishaw & Dunbar, 2000; Estrada et al., 2017, 2018; Isaac & Cowlishaw, 2004; Junker et al., 2017; Marsh & Chapman, 2013; Marsh, 2003; Nijman, Spaan, Rode-Margono, Wirdateti, & Nekaris, 2017; Schwitzer et al., 2017; Wich & Marshall, 2016). Unchecked human population growth and ensuing demands for resources through land conversion and agricultural expansion, and unsustainable economic development—in particular, rapid expansion of global road networks—have escalated these threats, further exacerbating declines in primate populations (Almeida-Rocha et al., 2017; Boonratana, 2013b; Chapman & Peres, 2001; Cowlishaw & Dunbar, 2000; Estrada et al., 2017, 2018; Isaac & Cowlishaw, 2004; Junker et al., 2017; Marsh & Chapman, 2013; Marsh, 2003; Schwitzer et al., 2017; Wich & Marshall, 2016). In recent decades, emerging threats such as climate change, and anthroponotic and zoonotic diseases have added more pressure on these primates and their habitats (Boonratana, 2013b; Estrada et al., 2017, 2018; Goldberg, Gillespie, Rwego, Estoff, & Chapman, 2008; Junker et al., 2017). Conservation efforts such as demarcating areas for protection, and including primates in national wildlife laws and policies, and international treaties and agreements, have had some degree of success (Boonratana, 2013b; Gaveau, Wich, & Marshall, 2016; Nijman, Nekaris, Donati, Bruford, & Fa, 2011; Estrada et al., 2018; Wich & Marshall, 2016). These interventions, however,

have not been able to completely arrest the decline in primate populations and their habitats (Boonratana, 2013b; Estrada et al., 2018; Gaveau et al., 2016). This has led to the employment of other complementary efforts such as awareness-raising, education, and socioeconomic assistance to marginalized societies living in or near primate habitats (Estrada et al., 2017, 2018; Junker et al., 2017).

An issue that further complicates primate conservation efforts is that numerous primate populations worldwide are currently persisting only in fragmented habitats, and this issue is likely to remain unabated (Estrada et al., 2017, 2018; Marsh & Chapman, 2013; Marsh, 2003). Some authors (Didham, 2010; Estrada et al., 2017; Fischer & Lindenmayer, 2007; Haddad et al., 2015; Laurance et al., 2018; Rogan & Lacher, 2018) consider habitat fragmentation and habitat loss as, currently, the leading two threats to terrestrial biodiversity and ecosystems. In fact, Taubert et al. (2018) even suggest that fragmentation of the world's tropical forests is nearly at the critical point of percolation, that is the point at which the rate of fragmentation will exacerbate radically. Obscuring the picture, there exist several variations as to how habitat fragmentation is defined and measured (see Didham, 2010; Fahrig, 2003). In this manuscript, fragmented habitats refer to those habitats that are (a) broken up into smaller distinct patches, exhibiting a reduced total area and isolation between the patches, or (b) dissected, but not isolated, and do not exhibit any significant reduction in the total area, for example, by a single-track road. Employing Urban, O'Neill, and Shugart (1987) definition of a landscape, in this paper, I refer to fragmented landscapes as fragmented habitats within a mosaic of heterogeneous landforms, vegetation types, and land uses.

The trend for primates living in more fragmented habitats or landscapes is unlikely to abate, and ongoing efforts to establish connectivity between fragmented habitats currently do not match the rate of decline of primates and their habitats, including even very large contiguous intact habitats (Boonratana, 2013b; Estrada et al., 2017, 2018; Marsh & Chapman, 2013; Marsh, 2003; Schwitzer et al., 2019). Therefore, there is an urgent need to better understand primates in fragments, including the variables that influence their viability, so as to develop the appropriate conservation responses.

There are a number of approaches towards understanding habitat fragmentation, its causes, and its consequences for species and ecosystems (Fahrig, 2003; Fischer & Lindenmayer, 2007; McIntyre & Barrett, 1992). In this manuscript, I describe a novel approach for identifying the causes and consequences of fragmentation on Asian primates by employing the IUCN-CMP Unified Classifications of Direct Threats Version 3.2 (IUCN & CMP, 2012). The IUCN-CMP Unified Classifications of Direct Threats Version 3.2 (IUCN & CMP, 2012) is a standard and precise lexicon for biodiversity conservation, and it is a universally known and widely accepted global scheme employed in several conservation-related analyses, as well as planning and management practices (Salafsky et al., 2008). However, this tool has not been utilized in terms of identifying the causes and consequences of fragmentation. I also describe a simple approach to rank the severity of threats, and I provide an indication of the significance of such threats to Asian primates in fragments. Employing these two approaches can provide guidance in the assessment of the type of threats faced by primate populations in fragments, as well as the development of appropriate conservation responses. In addition, I will identify and describe the specific variables that assist primate populations to survive/persist in fragments.

2 | METHODS

I assembled the information reviewed and analyzed in this manuscript from a collection of published and unpublished works relating to the conservation of Asian primate populations in fragments. The literature used in this manuscript, as well as personal observations, and methods employed in the analysis, do not in any manner violate the American Society of Primatologists' Principles for the Ethical Treatment of Nonhuman Primates.

To understand the specific causes and consequences of fragmentation, and to develop appropriate conservation responses, I adopt Salafsky et al. (2008) treatment of habitat fragmentation as stress, that is a degraded condition or degraded key attributes resulting from a direct threat. Furthermore, I interpret Salafsky et al. (2008) treatment of direct threats as anthropogenic activities or processes that destroy, degrade or impair biodiversity. Using this method, the first step is to identify the direct threats that can cause primate habitats to fragment. Hence, using this list (Table 1), I assessed the threats to Asian primates in terms of their likelihood as (a) causes of fragmentation, (b) variables that can exacerbate fragmentation, or (c) variables that can become threats to primates or primate habitats as a consequence of fragmentation. To achieve my goal in this assessment, first, I reviewed the list using my own research on primates and in primate habitats carried out across parts of Southeast Asia, South Asia, and East Asia (e.g., Boonratana, 2013a, 2013b; Boonratana & Le, 2013). Then, using the same list, I searched in established electronic journal databases and employed keywords that relate to the threats listed (e.g., "road," "railway," "electrocution," "agriculture," "oil palm"), those that relate to the subject (e.g., "fragments," "fragmentation," "primates," and the nomenclature of the Asian primate genera). For this analysis I considered Asian primates at the species level; only in some cases did I assess the subspecies.

In addition, I treat the severity of the threats to a primate taxon as the degree or risks of decline either in the taxon's population or its habitats; and I assessed the level of influence of existing or new threats as a consequence of fragmentation as (a) high, (b) moderate or (c) low. Threats assessed as high are those which threaten the persistence of the primate taxon under consideration; moderate are those that will likely threaten the persistence of the primate taxon in the near future, and low are those which are present, but unlikely to threaten the persistence of the primate taxon.

I also identified variables that can influence the survival of Asian primates in fragmented habitats from a review of both published and unpublished works (Table 2). Two aspects were considered when assessing primate population viability: the primate taxon's ability to maintain a viable population or resist further decline, and the ability of

TABLE 1 Causes of fragmentation, influencing variables exacerbating fragmentation, and consequences of fragmentation

Threats to biodiversity[a]	Threatens primates	Threatens primate habitats	Causes fragmentation	Exacerbates fragmentation	Threatens primate & primate habitats as a consequence of fragmentation
1. Residential & commercial development					
1.1 Housing & urban areas	Yes [L,M,H][b]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]
1.2 Commercial & industrial areas	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]
1.3 Tourism & recreation areas	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]
2. Agriculture & aquaculture					
2.1 Annual & perennial nontimber crops					
2.1.1 Shifting agriculture	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]
2.1.2 Small-holder farming	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]
2.1.3 Agro-industry farming	Yes [M,H]	Yes [M,H]	Yes [M,H]	Yes [M,H]	Yes [M,H]
2.2 Wood & pulp plantations					
2.2.1 Small-holder plantations	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]
2.2.2 Agro-industry plantations	Yes [M,H]	Yes [M,H]	Yes [M,H]	Yes [M,H]	Yes [M,H]
2.3 Livestock farming & ranching					
2.3.1 Nomadic grazing	Yes [L,M]	Yes [L,M]	No	Possibly	Yes [L,M]
2.3.2 Small-holder grazing, ranching or farming	Yes [L,M]	Yes [L,M]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]
2.3.3 Agro-industry grazing, ranching or farming	Yes [M,H]	Yes [M,H]	Yes [M,H]	Yes [M,H]	Yes [M,H]
2.4 Marine & freshwater aquaculture					
2.4.1 Subsistence/artisinal aquaculture	Yes [L,M]	Yes [L,M]	No	Uncertain	Yes [L]
2.4.2 Industrial aquaculture	Yes [M,H]	Yes [M,H]	Yes [M,H]	Yes [M,H]	Yes [M,H]
3. Energy production & mining					
3.1 Oil & gas drilling	Yes [M,H]	Yes [M,H]	Yes [M,H]	Yes [M,H]	Uncertain
3.2 Mining & quarrying	Yes [M,H]	Yes [M,H]	Yes [M,H]	Yes [M,H]	Possibly
3.3 Renewable energy	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Uncertain
4. Transportation & service corridors					
4.1 Roads & railroads	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]
4.2 Utility & service lines	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]
4.3 Shipping lanes[c]	Yes [L,M][d]	Possibly not	No	No	No
5. Biological resource use					
5.1 Hunting & collecting terrestrial animals					
5.1.1 Intentional use (species being assessed is the target)	Yes [M,H]	Yes [L]	No	No	Yes [M,H]
5.1.2 Unintentional effects (species being assessed is not the target)	Yes [M,H]	Yes [L]	No	No	Yes [M,H]
5.1.3 Persecution/control	Yes [M,H]	Yes [L]	No	No	Yes [M,H]
5.2 Gathering terrestrial plants					
5.2.2 Unintentional effects (species being assessed is not the target)	Yes [L]	Yes [L]	No	No	No
5.3 Logging & wood harvesting					
5.3.1 Intentional use: Subsistence/small scale	Yes [L,M]	Yes [L,M]	Yes [L,M]	Yes [L,M]	Yes [L,M]
5.3.2 Intentional use: Large scale	Yes [H]	Yes [H]	Yes [M,H]	Yes [H]	Yes [H]
5.3.3 Unintentional effects: Subsistence/small scale	Yes [L,M]	Yes [L,M]	Yes [L,M]	Yes [L,M]	Yes [L,M]
5.3.4 Unintentional effects: Large scale	Yes [H]	Yes [H]	Yes [M,H]	Yes [H]	Yes [H]

(Continues)

TABLE 1 (Continued)

Threats to biodiversity[a]	Threatens primates	Threatens primate habitats	Causes fragmentation	Exacerbates fragmentation	Threatens primate & primate habitats as a consequence of fragmentation
5.4 Fishing & harvesting aquatic resources					
5.4.3 Unintentional effects: Subsistence/small scale	Yes [L]	No	No	No	No
5.4.4 Unintentional effects: Large scale	Yes [L,M]	No	No	No	No
6. Human intrusions & disturbance					
6.1 Recreational Activities	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M]	Yes [L,M,H]	Yes [L,M,H]
6.2 War, Civil Unrest & Military Exercises	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]
6.3 Work & Other Activities	Yes [L]	Yes [L]	No	No	No
7. Natural system modifications					
7.1 Fire & fire suppression					
7.1.1 Increase in fire frequency/intensity	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]
7.1.2 Suppression in fire frequency/intensity	Yes [L,M]	Yes [L,M]	Yes [L,M]	Yes [L,M]	Yes [L,M]
7.2 Dams & water management/use					
7.2.1 Abstraction of surface water (domestic use)	Yes [L]	Yes [L]	No	No	No
7.2.2 Abstraction of surface water (commercial use)	Yes [H]	Yes [H]	Yes [H]	Yes [H]	Yes [L,M,H]
7.2.3 Abstraction of surface water (agricultural use)	Yes [L,M]	Yes [L,M]	Yes [L,M]	Yes [L,M]	Yes [L,M]
7.2.5 Abstraction of ground water (domestic use)	No	Yes [L]	No	No	No
7.2.6 Abstraction of ground water (commercial use)	Yes [L,M]	Yes [L,M,H]	No	Yes [L,M,H]	No
7.2.7 Abstraction of ground water (agricultural use)	Yes [L,M]	Yes [L,M]	No	Yes [L,M]	No
7.2.9 Small dams	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M]	Yes [L,M]	No
7.2.10 Large dams	Yes [H]	Yes [H]	Yes [H]	Yes [H]	No
7.3 Other ecosystem modifications	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]
8. Invasive & problematic species, pathogens & genes					
8.1 Invasive nonnative/alien plants & animals	Yes [L,M,H]	Yes [L,M,H]	No	No	Yes [L,M,H]
8.2 Problematic native plants & animals	Yes [L,M,H]	Yes [L,M,H]	No	No	Yes [L,M,H]
8.4 Pathogens & microbes	Yes [L,M,H]	No	No	No	Yes [L,M,H]
8.5 Viral/prion-induced diseases	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]
9. Pollution					
9.1 Household sewage & urban waste water					
9.1.1 Sewage	Yes [L,M]	Yes [L]	No	No	Yes [L]
9.1.2 Run-off	Yes [L,M]	Yes [L]	No	Yes [L]	Yes [L]
9.2 Industrial & military effluents					
9.2.1 Oil Spills	Yes [L]	Yes [L]	No	No	Yes [L]
9.2.2 Seepage from mining	Yes [L,M]	Yes [L]	No	Yes [L]	Yes [L]
9.3 Agricultural & forestry effluents					
9.3.1 Nutrient loads[e]	Yes [L]	Yes [L]	No	No	Yes [L]
9.3.2 Soil erosion, sedimentation	Yes [L]	Yes [L]	No	Yes [L]	Yes [L]
9.3.3 Herbicides and pesticides	Yes [L]	Yes [L]	Yes [L]	Yes [L]	Yes [L]
9.4 Garbage & solid waste	Yes [L]	Yes [L]	No	No	Yes [L]
9.5 Air-borne pollutants					

(Continues)

TABLE 1 (Continued)

Threats to biodiversity[a]	Threatens primates	Threatens primate habitats	Causes fragmentation	Exacerbates fragmentation	Threatens primate & primate habitats as a consequence of fragmentation
9.5.1 Acid rain	Yes [L,M,H]	Yes [L,M,H]	No	Yes [L]	Yes [L]
9.5.2 Smog	Yes [L]	Yes [L]	No	No	Yes [L]
9.5.3 Ozone	Yes [L]	Yes [L]	No	No	Yes [L]
9.6 Excess energy					
9.6.1 Light pollution	Yes [L]	No	No	No	Yes [L]
9.6.2 Thermal Pollution	Yes [L]	Yes [L]	No	No	Yes [L]
9.6.3 Noise pollution	Yes [L]	No	No	No	Yes [L]
10. Geological events					
10.1 Volcanoes	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	No
10.2 Earthquakes/tsunamis	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]
10.3 Avalanches/landslides	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]
11. Climate change & severe weather					
11.1 Habitat shifting & alteration	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]
11.2 Droughts	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]
11.3 Temperature extremes	Yes [L,M,H]	Yes [L,M]	Yes [L,M]	Yes [L,M]	Yes [L,M]
11.4 Storms & flooding	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]

[a]Only those that affect Asian primates are listed here.
[b]Level of influence of the threats to primate persistence, L = low; M = moderate; H = high.
[c]Shipping lanes here refers to motorized boats and barges plying major rivers and tributaries.
[d]Affects primate taxa that swim across rivers and tributaries on a regular basis for example, *Nasalis larvatus* (Boonratana, 2013a).
[e]Eutrophication also has known impacts on terrestrial wildlife that use the affected water bodies (Brooks et. al., 2016)

TABLE 2 Variables that influence population survival and viability of Asian primates in fragments, and the intensity of their influence

Variables	Conditions		
	Fragment-specific	Landscape-level	Primate-specific[a]
Fragment size	Yes [H][b]	–	–
Population size	Yes [H]	–	–
Native habitats	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]
Isolation	Yes [H]	Yes [H]	Yes [H]
Connectivity	Yes [H]	Yes [H]	Yes [L,M,H]
Shape	Yes [H]	–	–
Buffer zones	Yes [M,H]	–	–
Severity of edge effects	Yes [H]	–	–
Transport corridors	Yes [H]	Yes [H]	Yes [H]
Exposed power lines	Yes [H]	Yes [H]	–
Threats[c]	Yes [H]	Yes [H]	Yes [H]
Threatened status[d]	–	Yes [H]	Yes [H]
Protection status of habitats	Yes [H]	Yes [H]	Yes [H]
Behavioral/biological		–	Yes [H]
Ecological	Yes [H]	Yes [H]	Yes [H]
Human	Yes [L,M,H]	Yes [L,M,H]	Yes [L,M,H]

[a]Applies to the primate taxon or taxa whether occurring inside or outside the fragment.
[b]Intensity of their influence, L = low; M = moderate; H = high.
[c]Threats identified in Table 1.
[d]IUCN red list of threatened species.

the fragmented habitat to resist further degradation. I then followed by determining the *conditions* by which these variables operate and influence potential population survival. A condition, in this context, refers to whether a variable pertains to a whole landscape, a specific fragment, or a specific primate taxon. I classified the conditions that can influence primate population survival as those that have an (a) high, (b) moderate, or (c) low influence on primate population survival (Table 2). The level of influence can be applied to one or more Asian primate species.

3 | RESULTS

From a total of 75 threats to biodiversity (identified to the lowest level) listed in the IUCN-CMP Unified Classifications of Direct Threats Version 3.2 (IUCN & CMP, 2012), I assessed that 67 threatened the actual primates and 62 threatened their habitats (Table 1). Thirty-eight of these threats actually cause fragmentation, and 44 further exacerbate fragmentation. Of the 38 threats causing fragmentation, I assessed 30 as high, 35 moderate, and 28 low. Of the 48 threats exacerbating fragmentation, I assessed 32 as high, 35 moderate, and 34 low.

Fifty-three of these threats to primates and their habitats may be a consequence of fragmentation (Table 1). For example, consequences as diverse as invasive/nonnative flora and fauna, sewage, and light pollution are consequences of fragmentation that can all negatively affect primate populations in fragments (see Table 1 for complete list). I found 112 variables that represent potential new threats to primate populations affected by fragmentation of their habitats. Of these, 32 were serious, 36 moderate, and 44 represented relatively low threats (Table 1). Apparently, there were a higher number of threats from the consequences of fragmentation compared to direct threats.

I further determined 16 larger-scale variables that can influence Asian primate population survival in fragments (Table 2). The nature and significance of most of these varied according to the conditions under which they occur: the fragmented habitat, the landscape, or the specific primate taxon, population, and subpopulation.

4 | DISCUSSION

The IUCN-CMP Unified Classifications of Direct Threats Version 3.2 (IUCN & CMP, 2012) proves to be an effective tool for identifying and classifying immediate threats to Asian primates and their habitats. It is also useful in terms of comparing the causes and consequences of fragmentation. Similarly, assessing the severity of the fragmentation-related threats can effectively guide the prioritization of threats and conservation responses. This approach can result in a more meaningful assessment when examining the threats posed to a specific taxon or site. Furthermore, this assessment tool can be used by a range of conservationists (community members and other stakeholders, conservation practitioners, scientists, etc.) to improve prioritizing conservation initiatives at different scales. The information included in Figure 1 illustrates how the identification of the causes and consequences of fragmentation, and the understanding of underlying causes that drive the threats can assist in the development of appropriate mitigation measures (avoidance, minimization, rectification, reduction, and offsetting).

Table 1 illustrates that the fragmentation-related threats to Asian primates are more diverse than reported. In addition, many of these threats cannot be treated independently; one or more threats may influence or occur in association with another. Moreover, some threats, for example, pathogens and microbes and viral/prion-induced diseases, may increase in severity with fragmentation (Chapman, Gillespie, & Goldberg, 2005; Goldberg et al., 2008; Young, Griffin, Wood, & Nunn, 2013); and others, for example, light pollution (Hölker, Wolter, Perkin, & Tockner, 2010) and noise pollution (Duarte, Kaizer, Young, Rodrigues, & Sousa-Lima, 2018) may become new threats to primates whose habitats are now located along intact forest edges or in small fragments. Although identified as major causes of fragmentation, the significance of roads and railroads and utility and service lines have likely been underestimated (Hughes, 2018; Lawton, 2018); and have been noted to affect Asian primate persistence in fragments.

My assessment has also demonstrated that forest fragmentation is far more of a threat and stressor for Asian primates and their habitats than previously believed. Based on my assessment, I suggest

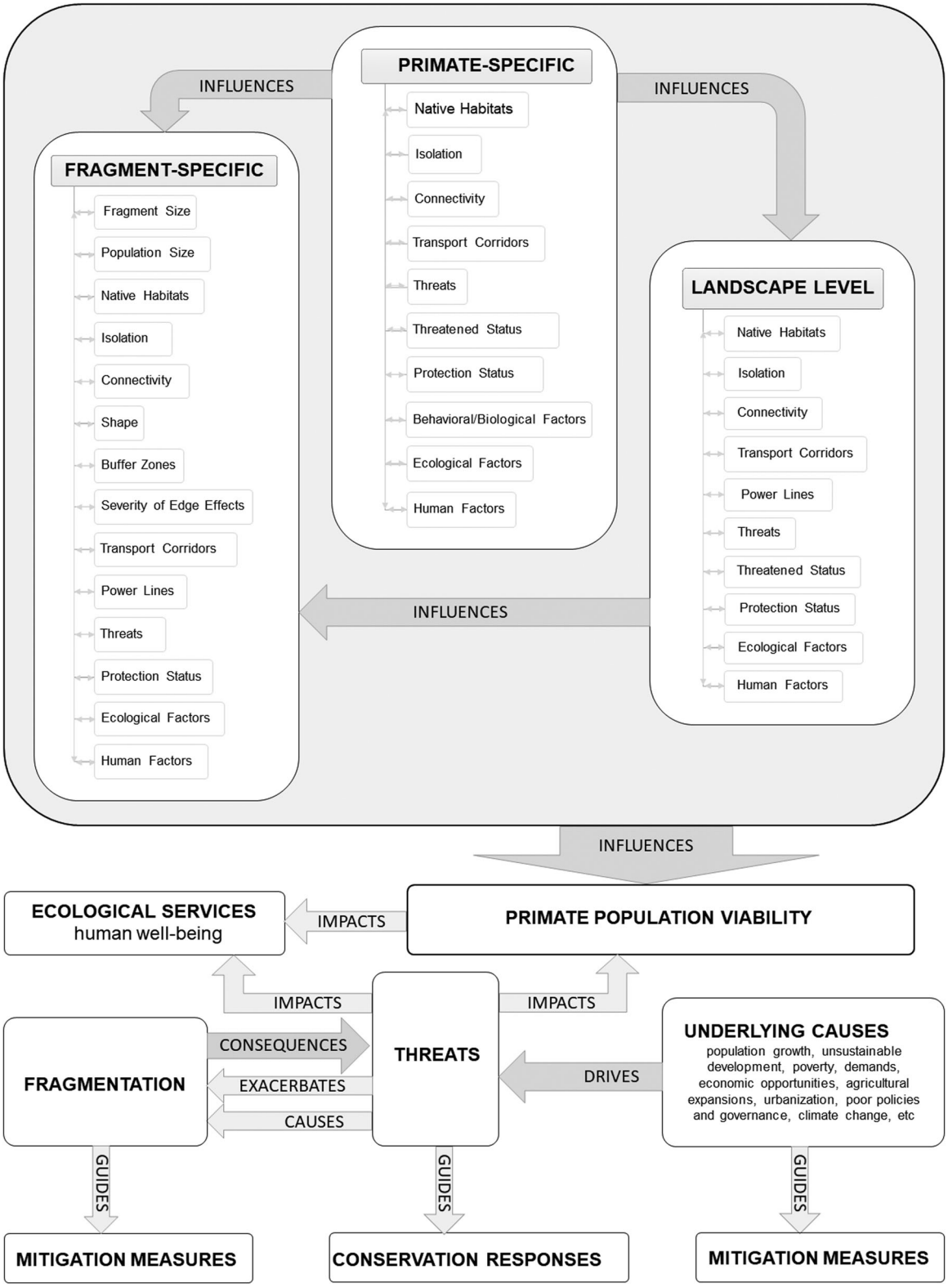

FIGURE 1 The threats of fragmentation and the variables influencing primate population viability. Threats causing and as a consequence of fragmentation, some underlying drivers to the threats, and how these threats impact primate population viability and ecological services; the inter-relationships between the variables and their conditions, and how they influence primate population viability in fragments; and how knowing specific threats, their causes and consequences, and their underlying causes can guide better the development of appropriate conservation responses and mitigation measures

that the type of threats exacerbating fragmentation as a consequence of habitat destruction greatly exceed those caused by initial fragmentation. As it is often difficult to avoid fragmentation associated with government-approved development projects, it is imperative that mitigation measures be developed at the outset. Adopting spatial planning practices and fragmentation impact assessments will facilitate such mitigation to a large extent.

Most literature (e.g., Fahrig, 2003; Haddad et al., 2015; Laurance et al., 2018; Marsh, 2003; Rogan & Lacher, 2018) points to the size of the fragment, edge effects, and the degree of isolation from other populations as key variables influencing species occupancy in fragmented habitats. In addition, given that studies on habitat fragmentation and conservation of biodiversity are often founded on the principles of island biogeography, much focus has been on size and isolation as predictors of species viability (Haddad et al., 2015, 2017; Laurance et al., 2018; Rogan & Lacher, 2018). Nijman (2013), for example, proposed that a fragment size between 50 and 400 km^2 is the minimum to support an entire Javan primate community, and further suggested that true rainforest species, such as the Moloch gibbon (*Hylobates moloch*), will be among the first species to experience extirpation after isolation. However, rediscovery of species previously considered extinct suggests that some species are able to persist in small and isolated fragments (Pimm & Jenkins, 2010). This is very likely possible only if certain conditions are met, for example, small isolated populations of the Tonkin snub-nosed monkey (*Rhinopithecus avunculus*) in Vietnam, once thought extinct, have persisted in remnant steep karst mountain habitats, as small as 10 km^2, right through much of the 20th century, only to be severely threatened with extinction in the recent decades due to high hunting pressure (Boonratana & Le, 2013). This example highlights that the conservation value of small and isolated fragments should not be underestimated. A number of authors (e.g., Boonratana & Le, 2013; Didham, 2010; Estrada et al., 2017; Fahrig, 2003) have clearly exhibited that any prediction of species viability must emphasize the variation in individual species' traits and responses, the characteristics of the habitat, the landscape (and the intervening matrix), and how these variables influence population persistence in fragments.

The properties and nuances found within the variables (Table 2) discussed here cannot be ignored, for example, less successful crossings are expected across a multilane, divided highway compared to a single-lane road. Multilane, divided highways expose primates to higher risks of injuries and casualties due to collision with vehicles (see Baskaran & Boominathan, 2010; Kumara, Sharma, Kumar, & Singh, 2000). Rivers, depending on their width and depth, serve as natural barriers to many primate taxa. Irrigation and drainage canals can similarly deter those primates that cannot swim or wade across them. In fragments and the intervening matrix, rivers that are used as transportation corridors can deter or disrupt even those taxa that can swim across them, for example, river crossings by proboscis monkey (*Nasalis larvatus*) and long-tailed macaque (*Macaca fascicularis*) along the Kinabatangan River and its tributaries (Boonratana, 2013a).

In particular, it is equally important to acknowledge that many of the variables discussed here can influence one another, for example, power lines (exposed or otherwise) are most often associated with highways and roads. A large-sized fragment lacking native or critical habitats is likely able to support a large population of generalist primates, but only a small population of ecologically sensitive primates, such as the proboscis monkey (Boonratana, 2013a). Proboscis monkeys are selective feeders, consuming large quantities of young foliage, and a significant proportion of flowers, unripe fruits, and seeds (Boonratana, 2003). They are also largely restricted to riverine, peat swamp, and mangrove forests of the coastal lowlands of Borneo (Boonratana, 2003). To the proboscis monkeys, the presence of even degraded riverside vegetation with trees overhanging the water bodies is more important than the presence of pristine native habitats (Boonratana, 2013a). Not all of their native habitats possess trees adjacent to or overhanging large water bodies. Although the proboscis monkeys use these habitats, their sleeping sites are restricted to those trees immediately adjacent to or overhanging large bodies of water (Boonratana, 2013a). Furthermore, although provisioning of primates (artificially) boosts population size, it is frequently carried out along roadsides in Asia, where speeding vehicles can pose a serious risk to primates that consume such foods. Observations regarding this problem have been noted in the northern plains sacred langur (Chhangani, 2004) and the rhesus macaque (*Macaca mulatta*; Pragatheesh, 2011) in India, as well as in the long-tailed macaque and northern pig-tailed macaque in Thailand (pers. obs.).

Simultaneously, it is important to consider the conditions under which the variables that I refer to occur, namely the habitat fragment, the fragmented landscape, as well as the ecological and behavioral/biological constraints or flexibility of the primates themselves (Table 2). For example, the presence of transport corridors and exposed power lines within protected habitat fragments will undoubtedly have far greater ramifications to primates and their fragmented habitats. Long-tailed macaques are, due to their widespread distribution and ability to occupy many types of habitats, probably the most common victims of vehicle collisions and electrocution from exposed power lines, especially in urban settings and along narrow transport corridors running through oil palm plantations (pers. obs.). The Department of Wildlife and National Parks of Peninsular Malaysia (https://www.wildlife.gov.my/index.php/en/) recorded the deaths of 439 long-tailed macaques, nine southern pig-tailed macaques, and 27 colobines killed in highway collisions in Peninsular Malaysia from 2012 to 2017. These numbers very likely represent a small portion of primates killed, as primates do not attract as much attention as larger, enigmatic, threatened species such as tigers and elephants, and are therefore rarely reported.

Examples of taxon-specific features in relation to highway crossings between fragments have been noted for the southern pig-tailed macaque (*Macaca nemestrina*) and the Raffles' banded langur (*Presbytis femoralis femoralis*) along the six-lane, divided Kuala Lumpur-Karak Highway at Genting Sempah in Malaysia. Road crossings by the terrestrial macaques were mostly successful with minimal fatalities, whereas such crossings by the arboreal langurs were primarily unsuccessful, with either several abandoned attempts or higher fatalities compared to the macaques (pers. obs.).

Finally, the viability of primates in fragments is also influenced by human attitudes (Aggimarangsee, 2013; Dela, 2011; Lee & Priston, 2005; Marsh & Chapman, 2013). In Asia, primates are tolerated by some and killed as pests, bushmeat, exotic delicacies or for purported medicinal properties by others (Boonratana, 2013b; Corlett, 2007; Estrada et al., 2017; Lee & Priston, 2005; Marsh & Chapman, 2013). Moreover, the degree of human tolerance to primates is highly variable, and frequently taxon-specific. In recent years, tolerance to primates has waned (see Campbell-Smith, Simanjorang, Leader-Williams, & Linkie, 2010; Dela, 2011; and Lee & Priston, 2005), and such intolerance can have significant impacts on several of the Asian primates. Even species such as certain langurs (e.g., *Semnopithecus entellus*, *S. priam*, and *S. vetulus nestor*) venerated by Hindus, are increasingly being killed for damaging crops (Dela, 2011; Lee & Priston, 2005; Perera & Vandercone, 2017). Figure 1 illustrates how the variables influencing Asian primate survival in fragments interrelate, and how their influence on primate survival is dependent on the conditions under which they operate.

In conclusion, future studies should aim to objectively evaluate and compare threats and consequences of fragmentation on Asian primates across populations and taxa, and attempt to predict primate population survival in relation to these threats. It is also important to consider past and current mitigation efforts to address such fragmentation and its effects. Equally significant, to achieve long-term and sustainable solutions for the conservation of primates in human-dominated fragmented landscapes, studies focused on understanding and integrating human dimensions are urgently needed. Given the diversity and complexity of human nature and human-modified landscapes, future studies, and evaluations must employ a multidisciplinary approach to be effective.

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CONFLICT OF INTEREST

The author declare that there are no conflict of interest.

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