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CONTRIBUTED PAPER

Severe human pressures in the Sundaland biodiversity hotspot

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Abstract

We assess the magnitude and the extent of recent change of significant human footprint within protected areas, key biodiversity areas and the habitat range of 308 lowland forest specialist birds in Sundaland, a global hotspot of biodiversity in Southeast Asia. Using the most recent human footprint dataset, we find that 70% of Sundaland has been heavily modified by humans. This represents a 55% increase in areas under intense human pressure since 1993. Areas under intense human pressure covered on average 50% of the extent of key biodiversity areas, 78% of each protected area and 38% of the range of lowland forest specialist birds. The results imply that the actual level of protection by protected areas is only one-third to half of that on paper once human footprint is accounted for. While all protected areas were impacted by human pressures, those managed strictly for biodiversity conservation presented the largest increases. These results highlight an exceptionally high human footprint across Sundaland and an impending further deepening of the biodiversity crisis across the region.

KEYWORDS

biodiversity, cumulative pressure, extinction, human footprint, IUCN protected areas, IUCN Red List

1 | INTRODUCTION

To reduce rates of biodiversity loss and achieve the United Nation's Convention on Biological Diversity Aichi

Biodiversity Target 11—that aims to have 17% of land area under protection—it is crucial to account for the type, distribution, and intensity of human pressure on the environment (Joppa et al., 2016). This information is

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crucial for informing action and policy to effectively conserve biodiversity (Geldmann, Joppa, & Burgess, 2014; Jones et al., 2018; Venter et al., 2016a). Methods to quantify the distribution and intensity of cumulative human pressures were first developed by Sanderson et al. (2002) in their work to map the terrestrial global “human footprint.” The individual pressures in the human footprint were selected and combined to represent the spatial pattern of human activities that negatively impact conservation status (e.g., Haines, Leu, Svancara, Scott, & Reese, 2008; Leu, Hanser, & Knick, 2008; Sanderson et al., 2002). One strength of the maps was their ability to visualize and interpret the complex, cumulative land-use dynamics into a simplified metric, and facilitate communication among policy makers, communities and scientists (Dennison, Lookingbill, Carruthers, Hawkey, & Carter, 2007; Haines et al., 2008).

The 2002 human footprint effort, however, failed to show up-to-date and temporal trends in human pressures. Recent advances in remote sensing have allowed for a reassessment of the distribution of these human activities through space and time (Venter et al., 2016a, 2016b), and a new human footprint with a total of eight variables representing direct and indirect pressures on the environment was recently generated for two time periods (1993 and 2009; Venter et al., 2016a, 2016b). The input data, ranging from the extent of the built environment, cropland, pastureland, population density, night-time lighting, railways, roads, and navigable waterways, are recognized as drivers of biodiversity loss (Maxwell, Fuller, Brooks, & Watson, 2016) and are strong predictors of species extinction risk (Crooks et al., 2017; Di Marco, Rondinini, Boitani, & Murray, 2013; Di Marco, Venter, Possingham, & Watson, 2018).

Evaluating changes in human footprint allows for the identification of finer level degradation and human pressures across landscapes and ecosystems (Jones et al., 2018; Watson et al., 2016), giving a more complete picture of the cumulative level of impact of human activities on biodiversity. As such, it is an important tool for monitoring the effectiveness of conservation interventions. For instance, changes in human footprint have been used to evaluate changes in human pressure within World Heritage Sites and protected areas (PAs) globally (Allan et al., 2017; Jones et al., 2018; Leroux et al., 2010), and to identify hotspots of wilderness loss (Watson, Jones, et al., 2016). Studies that comprehensively assess changes in human footprint across PAs and sites identified as critical for conservation (key biodiversity areas, KBAs) at a scale relevant for regional conservation decision-making are, however, scarce.

We carried out an assessment of human pressures across PAs, KBAs, and the ranges of 303 lowland forest-dependent bird species found in the biodiversity hotspot of Sundaland utilizing the latest human footprint data

(Venter et al., 2016a, 2016b). We chose lowland forest-dependent birds as lowland loss to cropland conversion is a large threat to biodiversity in Sundaland (Symes, Edwards, Miettinen, Rheindt, & Carrasco, 2018) and birds, being a taxa for which more accurate information on their distribution exists, could be used as a surrogate for other species loss (Larsen, Bladt, Balmford, & Rahbek, 2012). We chose Sundaland because of its high importance for biodiversity conservation and its high levels of threat. Sundaland comprises the Malay Peninsula, Borneo, Sumatra, Java, Bali and smaller islands on the Sunda Continental Shelf (Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000). Sundaland is recognized as a terrestrial global conservation priority based on a combination of its high species endemism and habitat loss (Myers et al., 2000; Polgar & Jaafar, 2018). Its unique geology and geography, with shallow waters bridging Australia and Asia, have permitted large levels of speciation through changes in sea level rise. As a result, Sundaland harbors over 15,000 endemic plant species, 115 endemic mammal species and 138 endemic bird species (Brooks et al., 2002). Over a third of Sundaland's birds are endemic to its distinct rainforests (Eaton, van Balen, Brickle, & Rheindt, 2016). Sundaland's forests face the highest rate of deforestation in Southeast Asia, which itself is characterized by the highest deforestation rates of tropical forests in the world (Hansen et al., 2013). The original primary vegetation of Sundaland has been reduced to only 7.8% of its original extent, from 1,600,000 to 125,000 km² as of 2000 (Polgar & Jaafar, 2018). Degradation of forests in the region occurs primarily due to selective logging, and deforestation is mainly due to intensive agriculture for food and fiber plantations (Wilcove, Giam, Edwards, Fisher, & Koh, 2013).

Here, we provide an assessment of changes in human footprint within PAs, KBAs, and bird ranges across Sundaland in Southeast Asia from 1993 to 2009. We define areas that are under intense human pressure using a threshold of human footprint ≥ 4 . The findings have implications for local and regional conservation initiatives, highlighting the fact that much of the entire region has been heavily modified by humans and little time remains for proactively conserving the last remnants of biodiversity in this unique biological hotspot.

2 | METHODS

2.1 | Assessing human pressure

To measure the extent of human footprint across Sundaland, we used the revised human footprint map (Venter et al., 2016a). The dataset maps at a 1-km² resolution eight human pressures for the years 1993 and 2009. The map

scores the individual pressures on a scale of 0–10 (not all pressures reach 10), based on their estimated relative impact on the environment, and then integrates these individual pressures to provide a human footprint score between 0 and 50 for each grid cell. The human footprint is recognized as the most accurate and comprehensive cumulative threat map available (McGowan, 2016). For the purpose of this study, we set the human footprint score ≥ 4 as a threshold criterion to determine if an area is under intense human pressure (Di Marco et al., 2013; Watson et al., 2016). A grid cell with a score ≥ 4 implies that there has been a significant intensity of human activity in the area, such that it can no longer be considered natural environment (Di Marco et al., 2013; Jones et al., 2018; Watson, Darling, et al., 2016). Recent analyses have noted that beyond this threshold, species are significantly more threatened by habitat loss and are at a higher risk of extinction (Di Marco et al., 2018).

2.2 | Protected areas and key biodiversity areas

We used the World Database on Protected Areas map (WDPA Consortium, 2018) to demarcate all PAs in Sundaland. For this study, we only included PAs established in or before 1993 to calculate the change in human pressure between the two time points: 1993 and 2009. We report the state of human pressure in all PAs in 2009. We considered only PAs that were nationally designated from IUCN (International Union for Conservation of Nature) Categories I to VI. We excluded PAs that did not have a polygon representation associated to them.

To study the dynamics of human footprint exerted on areas of high biodiversity and conservation value, we used the World Database of Key Biodiversity Area maps (International Union for Conservation of Nature, 2018). KBAs are recognized as one of the main pillars of conservation. To qualify as a KBA, an area must meet one or more criteria related to the presence of threatened biodiversity, geographically restricted biodiversity, ecological integrity, biological processes, and irreplaceability (Eken et al., 2004; Knight et al., 2007). We did not filter KBAs by date of establishment, as they do not directly influence on the ground management. As of 1993 there was about 20% overlap between PAs and KBAs. By 2009, there was 30% overlap.

2.3 | Ranges of lowland forest specialist birds

We obtained bird species distribution maps and their respective occurrence and habitat preference data from

BirdLife International and the Handbook of the Birds of the World (2016). This global dataset contains polygons for each bird range. The list of bird species was refined based on the occurrence in Sundaland (excluding vagrants), elevational preference (species with a majority of their range below 500 m) and forest dependency (as defined by BirdLife International) following Symes et al. (2018). Preferences for lower elevations and forest habitats were chosen to target the analysis to birds with a higher risk of extinction since lowland forests are the main target of deforestation in the region (Wilcove et al., 2013). After filtering based on the above criteria, a total of 308 lowland forest specialist bird species were used for analysis.

The geographical range for each species includes both suitable and unsuitable habitat and altitudinal ranges, making necessary that these ranges are refined to better reflect the extent of suitable habitat of the birds (Ocampo-Peñuela, Jenkins, Vijay, Li, & Pimm, 2016). To refine them, we restricted the range maps to show the extent of suitable habitat based on forest extent in Sundaland and the specific elevational range of each bird species (this condition was applied to the subset of species with elevational range below 500 m). Firstly, we clipped the species' range maps for forest extent in 2000 (Miettinen, Shi, & Liew, 2011) and 2015 (Miettinen, Shi, & Liew, 2016). The forest extent maps for 2000 and 2015 included the forest classes that ranged from primary up to degraded through selective logging: mangrove, peat swamp forest, lowland evergreen forest, lower montane evergreen forest, and upper montane evergreen forest (although this latter class was largely excluded via the altitudinal threshold applied).

The species' range maps were further refined to reflect the elevational ranges for each of the 308 bird species. We extracted each species' maximum and minimum elevation from BirdLife International (2016) and used the NASA Shuttle Radar Telemetry Digital Elevation Model (Jarvis, Reuter, Nelson, & Guevara, 2008) to clip the specified altitude for the range maps. We did not refine the range maps of species that did not have elevational data available. We performed all spatial analysis for bird ranges in Python 2.7.3 with tools provided by ArcGIS 10.3.1. Each of the 308 acquired maps was projected in the Equal Area Behrmann projection.

2.4 | Dynamics of human pressure in PAs, KBAs, and bird ranges

We overlaid the change in human footprint ≥ 4 with (a) PAs, (b) KBAs, and the (c) ranges of lowland forest specialist birds to measure the changes in human footprint across these features. We extracted the area within each of the biodiversity entities that either increased or

decreased in human footprint over the study period to gauge the change in threat within them. We used the nonparametric Mann–Whitney and Kruskal–Wallis tests to assess the statistical significance of the change. We assumed that the extent of suitable habitat map for each bird for 2000 was associated with human footprint in 1993 and the extent of suitable habitat map for 2015 was associated with human footprint in 2009.

2.5 | Effective coverage of protected areas

The IUCN categorizes PAs into six groups globally. Each category is based on different levels of protection and restrictiveness of use (Muñoz & Hausner, 2013). Categories I–IV are managed for biodiversity protection, while Categories V and VI also allow sustainable use of resources. These last two categories attempt to integrate conservation and resource extraction (Muñoz & Hausner, 2013). To quantify the effective extent of legal protection that KBAs and lowland forest specialist birds were afforded after accounting for human footprint ≥ 4 , we first calculated the area of the range of each species and area of KBA that overlapped with a PA of IUCN Category I–VI. We then updated this analysis deducting the areas that were under intense human pressure from the previously identified PAs.

3 | RESULTS

As of 2009, we found that 70.6% of the Sundaland biodiversity hotspot area faced human footprint ≥ 4 , that is, these areas can no longer be considered natural environments. The greatest concentrations were across Java, and generally towards coastlines (Figure 1a). PAs of Categories III, V and Ia presented the highest average percentage of area with human footprint ≥ 4 in 2009 (ca. 85–90%, Figure 2a) followed by Categories VI, IV and II (60–70%) and Category Ib (50%, Figure 2a). The Kruskal–Wallis test revealed that all human footprint changes within the PA categories was statistically significant ($p = 7.3 \times 10^{-11}$).

Approximately half (55.2%) of the Sundaland biodiversity hotspot showed an increase in the extent of areas under intense human pressure from 1993 to 2009, while only 10.6% of the biodiversity hotspot exhibited a decrease in the extent of areas under intense human pressure (Figure 1b). Increases in areas under intense human pressure were concentrated in Central Sarawak, Western, Central and Eastern Kalimantan, and in the region of Riau in Eastern Sumatra. While small pockets of reduction in areas under intense human pressure were situated in southwest Sabah and northwest

Peninsular Malaysia. The island of Java had no noticeable change in human footprint from 1993 to 2009. Additionally, Western Sumatra and Southern Sumatra had minimal changes in human footprint.

The changes in human footprint ≥ 4 (Figure 1b) seemed to explain the increases in cropland and human population density in Sundaland (Figure 1c,d). Overall, a substantial proportion of Sumatra experienced an increase in croplands. Reductions in croplands observed in southwest Sabah and northern regions of Peninsular Malaysia appeared to explain reductions in human pressures for those areas. Additionally, Western Java had reductions in cropland and increases in population density while Riau had large increases in population density (Figure 1c,d).

3.1 | Loss of intact areas within protected areas

In 1993, on average, $70.5\% \pm 38.6$ SD of each PA extent in Sundaland was categorized as having human footprint ≥ 4 , and this average increased to $77.9\% \pm 34.3$ SD by 2009 (Table S1 shows changes for individual PAs). The change in human pressures across PAs differed significantly ($p = .005$). The PA Category Ia showed the highest and a statistically significant increase (26.1%) in mean human pressure ($p = .0001$). The PA Categories Ib ($p = .49$) and VI ($p = .54$) experienced an increase in human pressure that was not statistically significant, whereas Categories II, III, IV and V remained stable (Figure 2a). Overall, this pattern speaks for a clear increase in human pressure within PAs of type Ia depriving a large fraction of their areas from their status as intact ecosystems.

3.2 | Human pressure within key biodiversity areas

Within KBAs across Sundaland, there was a mean increase of area under intense human pressure by $4.2\% \pm 19.1$ SD ($p = .07$). By 2009, an average of $27.4\% \pm 34.7$ SD of each KBA's area was categorized as facing human footprint ≥ 4 . About 84 (39.1%) of the KBAs exhibited an increase of areas under intense human pressure, whereas 33 (15.3%) exhibited a decrease of areas under intense human pressure (Table S2 shows changes for individual KBAs). The majority of KBAs showed no change over the 16-year period, mostly because they were already fully covered by areas with human footprint ≥ 4 (Figure 3).

On average, $27.4\% \pm 37.3$ SD of KBA area was protected by a PA of Category I–IV (Figure 4c). However,

97 (45.1%) KBAs remained completely unprotected by PAs of Categories I–IV. After excluding areas with human footprint ≥ 4 from PAs, the mean extent of protection in KBAs by a PA of Category I–IV fell to $9.5\% \pm 20.6$ SD and the number of KBAs that were completely unprotected raised to 135 (62.8%, Figure 4d).

3.3 | Human pressures in forest specialist bird ranges

Out of 308 lowland forest specialist birds studied, 273 (88.6%) experienced a reduction in their geographic range between 2000 and 2015. There was a significant mean reduction of $17.5\% \pm 6.1$ SD ($p = 5.38 \times 10^{-5}$) (Figure 5). A large portion of the ranges of lowland forest

specialist birds exhibited also an increase in human footprint during that period. Out of 308 species, 253 (82%) were characterized by an increase in areas where human footprint ≥ 4 in 2009 as compared to 1993 (Figure 5). The mean increase in range portions with human footprint ≥ 4 was $29.1\% \pm 175.6$ SD ($p = 1.40 \times 10^{-10}$) between 1993 and 2015.

Sabah Partridge (*Arborophila graydoni*) showed the highest increase in areas under intense human pressure within its geographical range. In 2000, only 224 km² (3.33%) of its original range exhibited human footprint ≥ 4 . However, by 2015, 5,500 km² (96.3%) within its range could no longer be considered a natural environment (Table S3). White-fronted Falconet (*Microhierax latifrons*) displayed the second highest percentage increase in areas under intense human pressure within the period

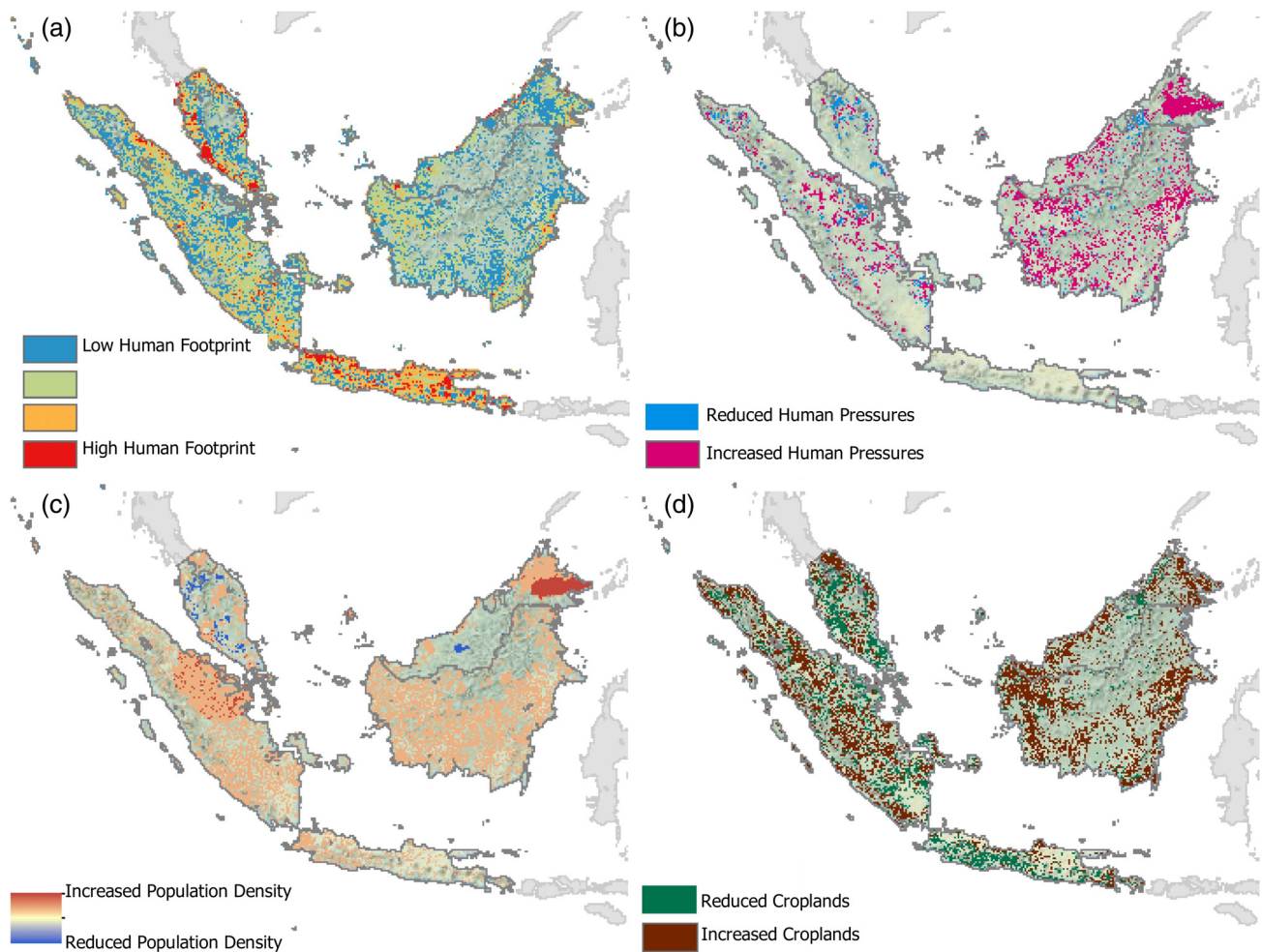


FIGURE 1 The distribution of human footprint in Sundaland. (a) Human footprint across Sundaland in 2009, with areas where the human footprint value is ≥ 4 . The range of human footprint score was divided across four brackets that included 4–10 (blue), 10–15 (green), 15–25 (orange), and 25–50 (red). (b) Distribution of human footprint change over the 16 years' time period (1993–2009) in Sundaland. Blue indicates regions that had a significant reduction in human footprint value to below 4 over time. Red indicates regions that had a significant increase in human footprint value to ≥ 4 over time. (c) Change in human population density over the 16 years' time period (1993–2009) in Sundaland. (d) Change in cropland distribution over the 16 years' time period (1993–2009) in Sundaland

(Figure 6). These species and the next two species with the highest increases (Figure 6) are all narrowly endemic to Sabah, an area on the island of Borneo characterized by high bird endemism but also some of the greatest increases in human footprint across the region (Figure 1).

Eight of the 10 bird species with the highest increases in areas under intense human pressure within their range are currently classified as near threatened (NT), one as least concern (LC) and only one as critically endangered (CR) (Figure 6, Table S3).

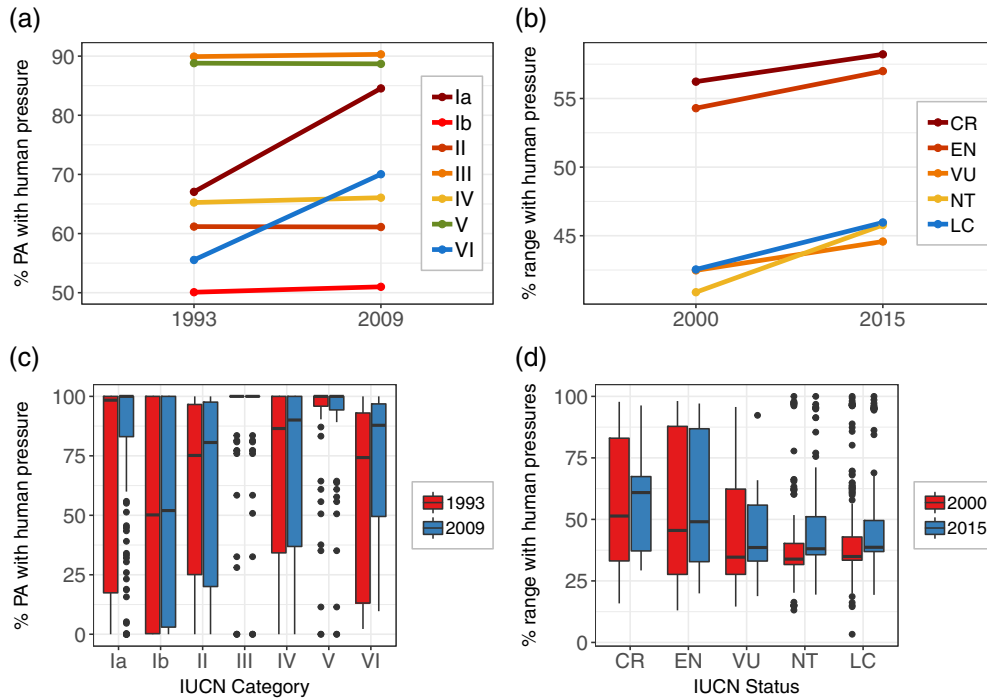


FIGURE 2 Changes in human footprint within protected areas (PAs) and in the suitable habitat of lowland forest-dependent birds. (a) Change in areas under intense human pressure (“human pressure”) (%) from 1993 to 2009 for PAs in Sundaland. IUCN PA categories: Ia, strict nature reserve; Ib, wilderness area; II, national park; III, natural monument; IV, habitat/species management area; V, protected landscapes; and VI, PA with sustainable use. (b) Change in the proportion of areas with intense human pressure within the range of 308 lowland forest-dependent bird species across Sundaland from 2000 to 2015. IUCN Red List status: critically endangered (CR), endangered (EN), vulnerable (VU), near threatened (NT) and least concern (LC). (c) and (d) represent (a) and (b) segregated based on IUCN category

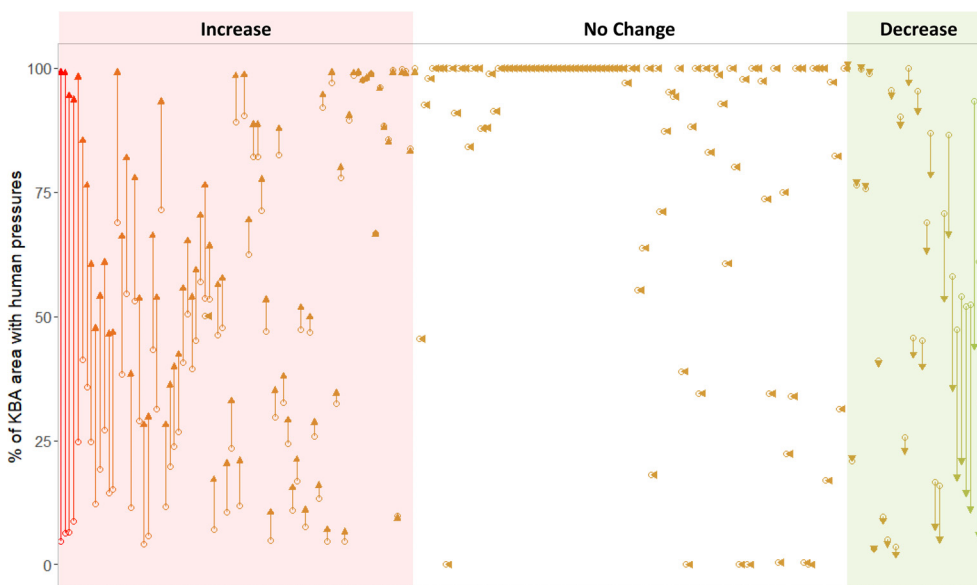


FIGURE 3 Change in area where human footprint ≥ 4 for 215 key biodiversity areas (KBAs) between 1993 and 2009 (“area with human pressures”). The circles represent the extent of human pressure in 1993 and the triangles in 2009. The lines drawn between the circles and triangles highlight KBA-specific changes

Overall, there was a substantial increase in the proportion of species' ranges classified as facing human footprint ≥ 4 for all IUCN Red List categories (Figure 2b,d). These increases in the proportion of range under intense human pressure ranged from 3.4 to 10.7% (Figure 2b). Higher levels of threat corresponded with higher human footprint within their ranges with CR species presenting the largest proportion of area under intense human pressure in 2009 (Figure 2d).

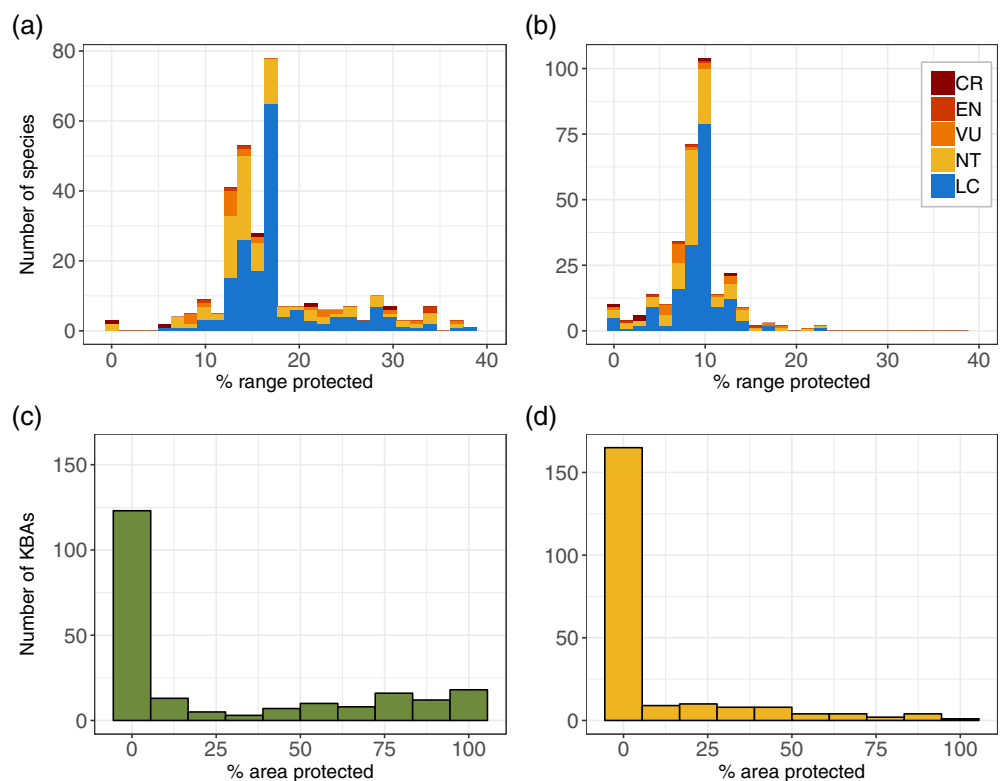
On average, $17.48\% \pm 6.56$ SD of the ranges of bird species was protected by a PA of Category I–IV (Figure 4a, Table S3). Red-breasted parakeet (*Psittacula alexandri*) was the most highly protected species, with 39.8% of its range falling within PAs. However, three forest specialist species were not protected at all: Nias hill myna (*Gracula robusta*) with IUCN status CR; Simeulue parrot (*Psittinus abbotti*) with IUCN status NT; and Simeulue scops-owl (*Otus umbra*) with IUCN status NT (Table S3). The three latter species are all small-island specialists endemic to the Western Sumatran island chain, indicating a lack of formal protection for the islands that comprise this important center of endemism. This dichotomy suggests substantial variation in the extent of protection for different species. On the other hand, there were no large differences in the extent of mean species protection among IUCN Red List categories: $14.4\% \pm 11.6$ SD for CR, $24.0\% \pm 12.7$ SD for EN, $16.9\% \pm 8.0$ SD for VU, $16.7\% \pm 7.1$ SD for NT, and $17.9\% \pm 5.4$ SD for LC (Figure 4b, Table S3).

When subtracting the proportion of area classified as facing human footprint ≥ 4 from within PAs of Categories I–IV, the mean extent of protection fell from 39.8 to 9.1%, resulting in the ranges of two additional species falling to 0% protection, namely the Javan fulvetta (*Alcippe pyrrhoptera*) with IUCN status LC and the White-breasted babbler (*Stachyris grammiceps*) with IUCN status NT, which amounts to an overall five species without any effective protection within Sundaland. Red-breasted parakeet's (*P. alexandri*) extent of protection fell from 39.8 to 18.3%, stripping it of its status as the most protected species in Sundaland (Table S3).

4 | DISCUSSION

Overall, the Sundaland biodiversity hotspot has been subjected to intense human pressure that compromises key conservation values in the region. On average, over 70% of protected land is under intense human pressures. This far exceeds the global average of approximately 30% due to the high concentration of human activities in Sundaland (Jones et al., 2018). Our results highlight that the distribution of human footprint is not uniform in Sundaland. For instance, areas of increases in human footprint were concentrated within Sabah, Riau, and Central Kalimantan. While the entire island of Java indicated no change in human footprint from 1993 to 2009, suggesting

FIGURE 4 Histogram of the number of key biodiversity areas (KBAs) and bird ranges against the percentage of area that fell within a protected area (PA; IUCN Category I–IV) in 2009. (a) and (c): the percentage of birds' extent of suitable habitat and KBAs within PAs, respectively. (b) and (d): the percentage of KBAs and birds' extent of suitable habitat protected within PAs without human footprint ≥ 4



that the region has been under intense human pressure since 1993, with no areas remaining in a natural state.

Our results also show that KBAs, PAs and bird species' ranges experienced a dramatic increase in human footprint from 1993 to 2009. These conclusions attest to a much lower actual level of effective protection in Sundaland as compared to the theoretical extent of areas protected once human footprint is accounted for. Despite the overall increase in human footprint, its distribution was not uniform across Sundaland. For instance, increases in areas under intense human pressures within Sumatra and Kalimantan were predominantly concentrated in Riau (excluding the Pelalawan Regency) and Central Kalimantan. Much of this can be explained by the large expansion in oil palm plantations, which almost doubled in extent from 1990 to 2010 at the expense of forested land in Central Kalimantan (Gaveau et al., 2013) and increases in population density (Figure 1c). Although forest-dependent birds can still occur in degraded forests (e.g., twice logged forests), monoculture plantations are particularly detrimental for their survival (Edwards et al., 2010; Edwards, Edwards, Hamer, & Davies, 2013).

One of our key findings was that the majority of PAs in Sundaland experienced a pronounced increase in areas under intense human pressure so that large fractions of these PAs can no longer be considered natural environments. This result concurs with past studies reporting that at least 6.5% of forest loss occurred in parts of Kalimantan and Sumatra where clearing forest is prohibited (Broich et al., 2011). For instance, the Bukit Barisan Selatan National Park in southern Sumatra, which forms part of the Tropical Rainforest Heritage of Sumatra Natural World Heritage Site experienced large-scale habitat loss (up to 10% of its forested area; Allan et al., 2017) due to agricultural encroachment by coffee plantations since 2001 (Gaveau et al., 2012). This apparent mismanagement of PAs might be due to a lack of funding available for PA management in Indonesia even in a World Heritage Site (Ministry of National Development Planning of the Republic of Indonesia, 2016).

The official proportion of area covered by PAs in Indonesia and Malaysia is 12.17% and 19.12%, respectively (The World Database on Protected Areas, 2018). These figures would indicate that Indonesia is on its way to achieving, and Malaysia has already achieved, the Aichi Target 11 established by the Convention on Biological Diversity, which stipulates that 17% of land area be under protection to safeguard against biodiversity loss. However, our results suggest that for KBAs and bird ranges, the actual protection after deducting areas under intense human pressure may only be one-third and half of the official protection, respectively. This implies that Indonesia would be a long way from achieving, and Malaysia would not yet have achieved Aichi

Target 11, which includes the provision that PAs must be effectively managed. These results are concordant with recent research identifying that one-third of the area within global PAs is under intense human pressure and, as such, the actual level of protection offered by the current PA network is much lower than expected (Jones et al., 2018).

Our analyses revealed that the coverage of KBAs and ranges of lowland forest specialist birds by PA Categories I–IV was sparse across Sundaland. KBAs in Sundaland are primarily located in biodiversity-rich lowland forest. PA allocation in Sumatra and other regions in Sundaland, by contrast, favors highland areas, leaving the

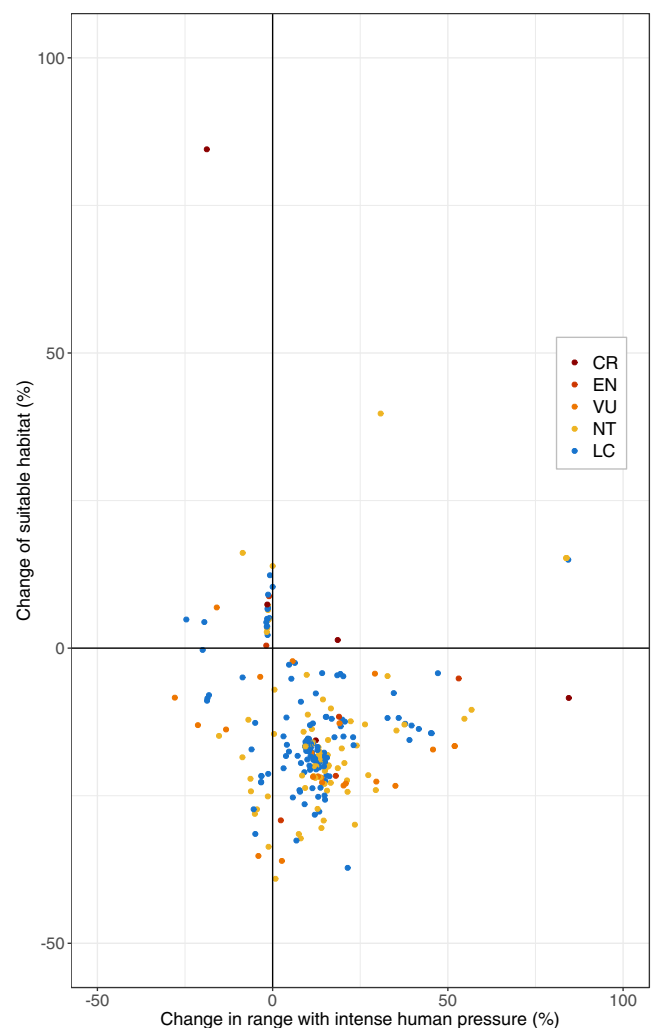


FIGURE 5 Percentage change in species extent of suitable habitat versus change in area under intense human pressure within the species' extent of suitable habitat. The species are colored according to their IUCN status. Majority of the birds are situated in the quadrant where the range is decreasing and the area under intense human pressure within their range is increasing. The figure does not include six species whose percentage change in area under intense human pressure and range was beyond the axes limits

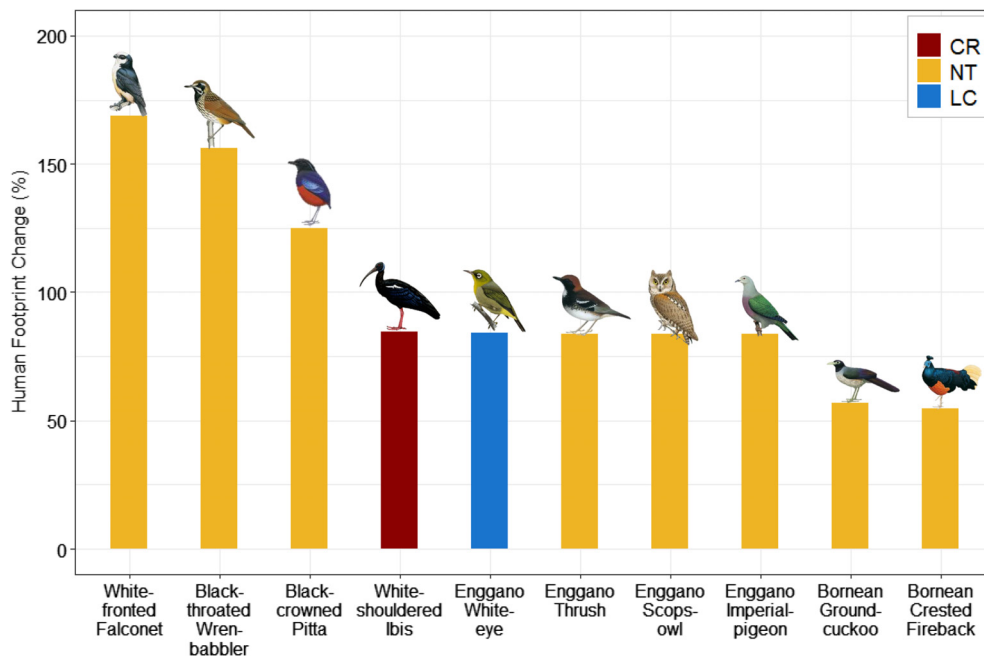


FIGURE 6 Top 10 lowland forest specialist bird species with the largest increase in range portions with human footprint ≥ 4 between 2000 and 2015. The figure excludes Sabah Partridge (*Arborophila graydoni*), a species IUCN-listed as Least Concern that showed the greatest increase in areas under intense human pressure within its range at 2793%. IUCN Red List status: critically endangered (CR), near threatened (NT) and least concern (LC). Species illustrations are not within the CC-BY license of this publication, and instead are reproduced from del Hoyo, Elliott, Sargatal, Christie, and de Juana (2018)

biologically diverse lowland forests unprotected (Joppa, Loarie, & Pimm, 2008). This trend reflects the importance afforded to extractive forest industries that are more profitable in lowland forests (Gaveau et al., 2009) and is mirrored by a decline in lowland forest PAs by more than 56% from 1985 to 2001 due to timber and plantation concessions in Kalimantan (Curran et al., 2004).

The greatest increase in areas under intense human pressure within Sundaland occurred in IUCN Category Ia PAs, which are supposed to provide the highest level of biodiversity protection. Leroux et al. (2010), similarly found that IUCN Category Ia had a higher proportion of human footprint values compared to Category Ib used static human footprint values for the year 2000 to evaluate the degree of naturalness in PAs at a global scale. Our results additionally reveal that the level of human pressure within Category Ia was higher than that of all other categories at a regional scale. These results are in contrast with global analyses that identify Category Ia as more effective at reducing increases in human pressures (Jones et al., 2018). This suggests that PA enforcement is weaker in Sundaland and local dynamics are especially threatening to biodiversity. For instance, strictly PAs of Category Ia in Indonesia are reported to suffer accelerated levels of deforestation. By contrast, managed logging concessions are more effective at preventing deforestation (Brun et al., 2015), a result also observed in Kalimantan's

natural forests (Gaveau et al., 2013). Within their concessions, companies have a greater capacity to prevent illegal logging, which allows reducing deforestation. Thus concessions render, paradoxically, a means by which the forest can pay for its own protection (Leroux et al., 2010).

Yet, there are also success stories of PA gazettement and enforcement in Sundaland. We also found that areas across Sundaland that have witnessed decreases in their human footprint (Figure 1b). These reductions appear associated to reduced cropland extension that could respond to enhanced protection (Figure 1d). An example of human footprint reduction is the Belum-Temengor forest complex in the Peninsular Malaysia, near the border with Thailand. The state government of Perak gazetted 1,175 km² as a state park in 2007 (Bernama, 2007). A similar example is the reduced human footprint areas in Endau Rompin National Park, gazetted in 1993. The establishment of these PAs thus explains the reduction in human footprint through their enforcement, demonstrating that the establishment of PAs can contribute to protect biodiversity.

Our results underscore that changes in the dynamics of human pressure across Sundaland have contributed to a reduced range of the majority of lowland forest specialist birds. This is primarily due to forest cover reduction coupled with an increase in the proportion of human

pressure within their ranges. These dynamics could affect the long-term survival prospects of many birds, especially considering that over one-third of the birds in Sundaland are endemic to lowland forests (Eaton et al., 2016). In Sundaic songbirds, this threat is particularly detrimental because of its dangerous synergy with the pressure of unsustainable illegal trade (Symes et al., 2018). Keeping songbirds as pets is a popular hobby especially in Indonesia that has a centuries-old tradition that has intensified in volume in the most recent decade with increasing affluence (Shepherd, 2006). The change in specific human pressures within the human footprint dataset could be used to gauge the extent of the threat posed by the pet trade. For instance, an increase in population growth has been linked to the increase in the threat to Indonesia's wild birds (Jepson, 2010).

Our approach allowed us to flag particular areas in Sundaland that are especially affected by an increase in human footprint. For instance, the top four species with the largest increase in range portions affected by human pressure are all from Sabah. This finding reflects two colliding realities: (a) Sabah is a major center of endemism for birds and other vertebrates in Sundaland, with a wealth of species that are narrowly restricted to this state (Eaton et al., 2016); (b) at the same time, Sabah has suffered some of the greatest increases in human footprint over the last few decades (Figure 1). Many of the species flagged as having suffered from the greatest increase of human footprint are currently not even recognized under any IUCN threat category. This trend highlights an urgent need to re-assess the threat to Sabah endemics. Similarly, we found that all three species whose range is completely unprotected constitute small-island specialist birds that are narrowly endemic to the West Sumatran island chain, highlighting a gross oversight in Sundaland's network of PAs that completely overlooks the important center of endemism along the West Sumatran island chain.

Our analyses were subject to multiple caveats worthy of discussion. The human footprint maps used to set a threshold for human pressure do not account for other pressures such as wildlife poaching, songbird trapping, invasive species, and climate change (Wilcove et al., 2013). For instance, our analysis overlooked possible lower elevational birds that could gain an increase in range due to the upslope movement in response to climate change. However, the pressures incorporated are often closely associated with many of these threats. For instance, changes in accessibility indicated by night-lighting, railways, human population density and roadways are good proxies for increased poaching and trapping (Venter et al., 2016a). This suggests that our

analysis is a conservative assessment of human pressure on biodiversity. Another caveat is that the original population density maps used in the human footprint maps may have been interpolated at the census level for administrative units in areas where spatially explicit data are sparse. This could have led to misidentifying changes in human footprint in isolated areas in the region. However, our approach, using the best data available, still provides an overview on the impact of human footprint in the region. Future research collecting data on the ground for specific biodiversity entities would need to be carried out to complement our large-scale research.

The methodologies used to develop the 2000 and 2015 forest extent maps were slightly different. The 2015 map included a wider level of disturbed forests in the forest classes, whereas the 2000 map did not (Miettinen et al., 2016). While this disparity makes the estimation of suitable habitat loss conservative, it may render the analysis of changes in human footprint less conservative as we are likely to include more areas under intense human pressure in the habitat lost by the birds in later years. Finally, the use of the threshold of human footprint ≥ 4 may not offer reward to restoration and protection enforcement interventions unless an "intact" status is regained. A continuous gradient analysis would help identify actions that are progressing towards reducing the human footprint, yet the threshold has been shown to be an adequate measure of biodiversity threat (Di Marco et al., 2018).

Our results indicate that human footprint is extensive and has rapidly increased across PAs, KBAs, and bird ranges in a short period of 16 years, depriving much of their area from their status as natural environments. This threatens to undermine PAs from achieving their primary conservation objective of protecting threatened species. In addition, forest-dependent bird species will likely decline in portions of their ranges under high human footprint. The results further demonstrate that conservation efficacy across Sundaland is drastically overestimated as the actual level of protection by PAs is much lower (one-third to half of that on paper) once human footprint is accounted for. This trend could be reflective of other regions in the world and would require further research. If governments do not take rapid proactive conservation action to retain these last intact ecosystems across the region, a globally significant extinction crisis will likely occur.

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CONFLICT OF INTEREST

The authors declare that they do not have any conflict of interest.

AUTHOR CONTRIBUTIONS

M.V., L.R.C. and J.E.M.W. designed the research. M.V. performed the research. K.J., J.R.A., O.V., F.E.R., D.P.E. provided technical expertise. M.V. wrote the first draft of the article. All authors contributed to write the subsequent drafts of the article.

DATA ACCESSIBILITY STATEMENT


All data and software code are freely available either within the supporting information document, or available at the referenced sources.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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