

# Conservation science in the tropics: why so much ecological research is useless, and why we need more of it

## Introduction

Recent years have seen considerable discussion of mismatches between published conservation science and the information needed to achieve tangible conservation results (e.g., Meijaard and Sheil, 2007; Whitten et al., 2001). As an academic, I am personally far from satisfied with my own ability to ensure that the results of my field studies are directly relevant to preserving threatened species and habitats. Nevertheless, I firmly believe that good ecological science can, indeed must, play a role in conservation. I sense that I am not alone in my ambivalence. In fact, I perceive that the tension between on the one hand striving to do sound ecological research that will contribute to conservation and on the other harboring nagging doubts about whether we are really making a difference runs through much of academic conservation science. In this chapter, I discuss several empirical results that bear on this tension. I first explore some broad trends across the paleotropics and consider how well our research is aligned with the real needs of conservation. I then discuss how long-term studies of orangutans at multiple sites can help place in appropriate ecological context recent work on orangutans in timber concessions and industrial plantations. Finally, I provide two simple examples of how basic ecological research can provide non-trivial insights that can inform more applied conservation.

## Distribution of research in the Paleotropics

The tropics are highly diverse, poorly understood, and direly threatened. Primatologists are well positioned to help address both ignorance of and threats to the topics. Our research contributes disproportionately to understanding of tropical ecology (Marshall and Wich, 2016a; Marshall et al., 2016a) and the information we gather can, at least in theory, contribute to more effective conservation and management (Chapman and Peres, 2001; Cowlishaw and Dunbar, 2000; Marshall and Wich, 2016a, 2016b). It is also becoming increasingly clear that researchers provide direct protective benefits at many

sites, reducing threats by building local capacity, heightening awareness, providing alternative incomes, enhancing law enforcement, and more (Campbell et al., 2011; Laurance, 2013; Tranquilli et al., 2012; Wrangham, 2008). Although the evidence to date has been largely anecdotal, it is becoming increasingly clear that researchers can make positive contributions at their research sites, and quite often do. Our knowledge of where tropical researchers work and why they work there is, however, quite limited.

Knowing where researchers work is relevant to understanding the spatial distribution of the protective benefits from research and assessing the extent to which the understanding we gain from our research might contribute positively to conservation (Kier et al., 2005; Martin et al., 2012). To determine the geographic distribution of research in the Paleotropics, my collaborators and I focused on protected areas in all African and Asian countries that contain great apes (Marshall et al., 2016a). We used the number of hits returned by a Google Scholar search of the name of each protected area as a proxy for research effort at each of the 565 protected areas in these 23 countries (see Marshall et al., 2016a for details on all methods). Analysis of online searches is widely used to assess interest in specific topics, including environmental and conservation issues (Mccallum and Bury, 2013; Meijaard et al., 2012, 2015; Sitas et al., 2009). We selected Google Scholar as a proxy of research attention because it indexes a wider array of published sources – including conference proceedings, management reports, and non-English language articles – than other popular scholarly databases (Meho and Yang, 2007). We used the World Database of Protected Areas (WDPA; [www.protectedplanet.net](http://www.protectedplanet.net)) and other published sources to record the size, International Union for Conservation of Nature (IUCN) management category (e.g., National Park, Species Management Area), and year the area was gazetted in its current designation. We also recorded the presence or absence of great apes in each protected area using a variety of published sources and personal correspondence with knowledgeable individuals.

### *Variation among protected areas*

Our searches returned over 52,500 Google Scholar hits and demonstrated huge variation in the allocation of research effort across Paleotropical protected areas (Figure 1). Ten percent of sites accounted for 85% of Google Scholar hits in Africa and 46% in Asia. Sites with the highest number of hits in Africa were the Serengeti (hits = 4,880), Kibale (3,370), and Gombe (3,290) National Parks. Gunung Mulu (1,270), Gunung Leuser (825), and Kerinci Sebalat (720) National Parks returned the most hits among Asian sites. In Africa, more than a third of protected areas returned no hits at all, while more than half returned fewer than five hits. Patterns were less pronounced in Asia, although still highly skewed, with over a fifth of protected areas returning no hits and more than a third with fewer than five (Marshall et al., 2016a). These results suggest that most of what we know comes from a very small number of sites and that we know almost nothing about many protected areas. Our knowledge is remarkably spatially limited.

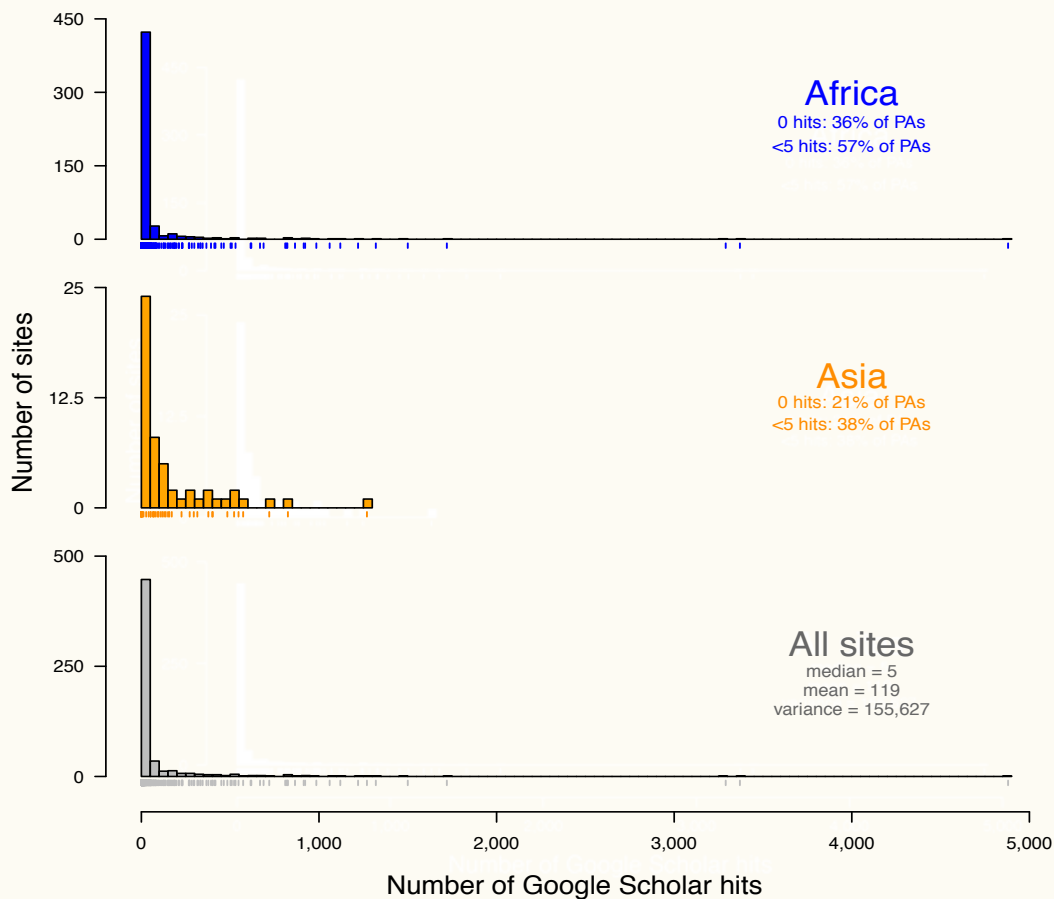


Figure 1. Histograms of the number of Google Scholar hits per protected area. Panels depict protected areas (PAs) in Africa ( $n = 512$  protected areas, top), Asia ( $n = 53$  protected areas, middle), and the full sample ( $n = 565$  protected areas, bottom).

### *Variation among countries*

We also recorded vast differences in research investment among countries, with the average number of hits per protected area differing by many orders of magnitude (Figure 2). Full consideration of the possible explanations for these differences is beyond the scope of this chapter, but as a preliminary exploration I conducted a simple analysis to assess the effects of obvious potential predictors. I calculated for each country both the mean and median number of Google Scholar hits per protected area and used these as dependent variables<sup>1</sup>. I compared a series of linear models of the  $\log(\text{mean})$  number of hits and a series of negative binomial models for the median number of hits. In both analyses, I compared models predicting a country's hit counts based on various combinations of area<sup>2</sup>, population size<sup>3</sup>, population density<sup>4</sup>, per capita gross domestic product (GDP<sup>5</sup>), Democracy Index (DI<sup>6</sup>), Human development index (HDI<sup>7</sup>), the Worldwide Governance Indicator on Political Stability and Absence of Violence/Terrorism, SAFE<sup>8</sup>), and whether English was a *de jure* or primary spoken language<sup>9</sup>. As this was an exploratory analysis that I conducted with no *a priori* hypotheses in mind, I compared all possible combinations of these variables using the 'dredge' function in the package {MuMIn} ver 1.40.4 (Bartoń, 2018) in R 3.4.3 (R Core Team, 2017).

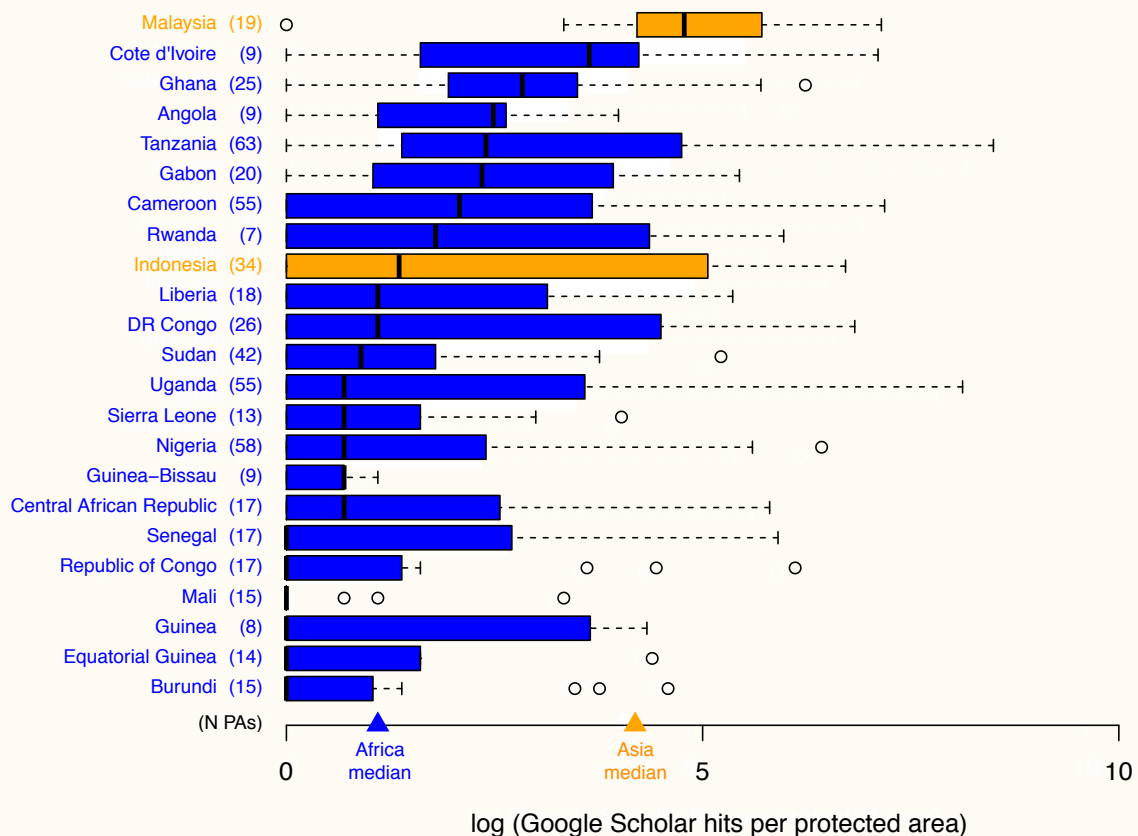


Figure 2. Boxplots of log (Google Scholar hits per protected area) by country. Orange and blue indicate African and Asian countries, respectively. Sites are listed from top to bottom in order of decreasing median hit counts per protected area– for countries with identical median values (e.g., Guinea, Equatorial Guinea, Burundi, for which the median hit counts were zero), they are ordered in decreasing order of mean hits. The number of protected areas per country are listed in parentheses after the country names.

To summarize predictors of mean hit counts, I used AICc model weights to build an averaged model comprising all models with  $\Delta\text{AICc} < 3$ . In this averaged model, mean Google Scholar hits per protected area were predicted by (in order of decreasing importance) population size, HDI, GDP, and SAFE; larger values for HDI, population size, and SAFE were associated with more hits while per capita GDP had a negative effect. Area, population density, DI, and use of English were not reliable predictors of mean hit counts. As my model for median hit counts was a negative binomial generalized linear model (GLM), calculating averaged coefficients is inappropriate<sup>10</sup>. Thus, I examined the role of predictors in each of the top models. The most important predictor was HDI, which had a strong positive effect, followed by important positive effects of SAFE, area, population size, and GDP. The overall results of the two analyses were similar, with the exception of GDP, which had a negative effect in the mean model and a positive effect in the median model. This is explicable because both Tanzania and Uganda, with relatively low per capita GDP, were rated highly in mean hit counts due to extreme outliers. The analysis of median counts is less sensitive to these outliers. These simple analyses suggest that research effort tends to be focused disproportionately in large, populous countries with relatively high ratings for human development, political stability, and safety. The fact that most research comes from places that rate relatively highly for these

positive attributes is unsurprising, but it does suggest that the conclusions we draw from the results of our research may not apply in all contexts.

### *Variation in taxonomic content*

My colleagues and I also assessed the taxonomic content of papers from a randomly sampled 20% of protected areas in our sample (Marshall et al., 2016a). We found that research was strongly biased towards a small subset of biodiversity. For example, great apes were the most commonly studied taxon, followed by non-primate mammals and non-ape primates. Mammals comprised over 70% of hits, a percentage far greater than the portion of total tropical diversity comprising mammals. Plants were the focus of 11% of studies and birds 6%. Interestingly, almost half of papers focused on primates, suggesting that primatologists are contributing a huge amount to our overall understanding of the tropics. These results suggest that our knowledge of the tropics is largely confined to a limited set of taxa.

### *Predictors of variation among protected areas*

Google Scholar hit counts were higher for protected areas that were larger, gazetted as national parks, and contained great apes (Marshall et al., 2016a). Our top models (based on AIC) all included a random effect for country and indicated that park size had a positive effect on hit counts. Protected areas gazetted as national parks returned 15 times as many hits as otherwise comparable parks with different IUCN designations. While the presence of any ape was associated with a roughly threefold increase in overall hits, our top models included separate predictors for each ape taxon. Protected areas with gorillas received 35 times as many Google Scholar hits as protected areas of comparable size and IUCN designation that lacked them. Orangutans, chimpanzees and bonobos were associated with increases in hit counts of 3.8, 2.3, and 1.4 times respectively, controlling for park size and IUCN designation. This analysis demonstrates that most knowledge we have about protected areas in the Paleotropics comes from large national parks containing great apes.

### *Is research focused in protected areas?*

To make our analysis tractable, we focused on protected areas in the Paleotropics, excluding any work conducted outside protected areas. Before considering the broader implications of the distribution of research effort across protected areas, it is worth considering what proportion of total research effort is expended inside protected areas. As a preliminary assessment of the overall distribution of research effort, I focused on field studies of great apes. For each of the four broad ape taxa, I did an exact phrase Google Scholar search for the taxon name (e.g., “orangutan”, “gorilla”) and for the first fifty field studies that were returned recorded whether the fieldwork was conducted inside, outside, or both inside and outside a protected area<sup>11</sup>. Overall, 78% (range 70%–84%) of returned field studies were conducted inside protected areas, 17% in non-protected areas (range 10%–24%), and 6% in both (range 2%–8%). The

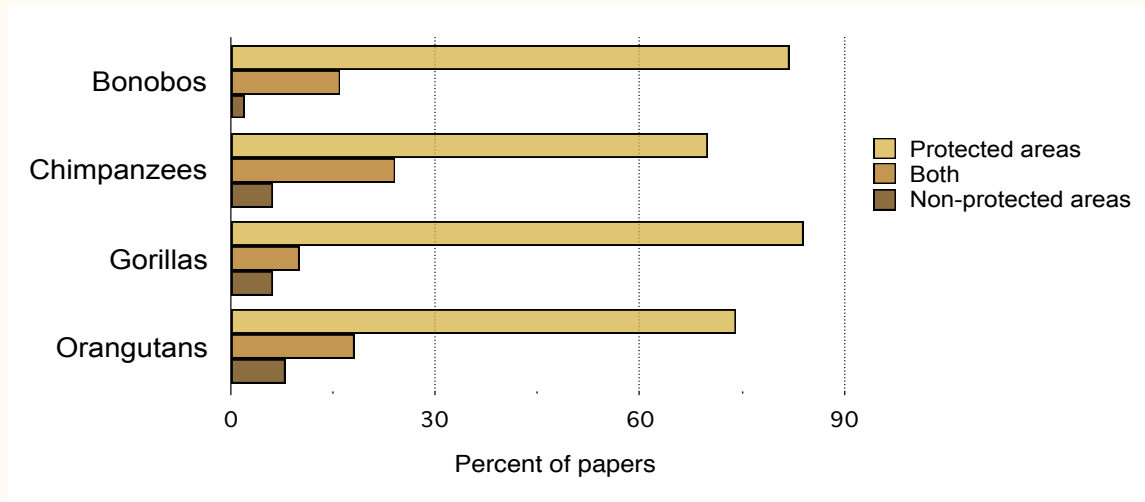


Figure 3. Distributions of field studies of wild apes, indicating whether studies were conducted inside protected areas, outside protected area, or in both protected and unprotected areas.

relative allocation of research effort did not differ greatly among ape taxa. Gorillas were the most heavily biased, with 84% of returned field studies being conducted inside formally designated protected areas (followed by bonobos (82%), orangutans (74%), and chimpanzees (70%); Figure 3). This simple analysis suggests that most research is conducted inside protected areas, indicating that the patterns we found above may apply to most field research conducted in the tropics.

### *Implications of research allocation*

These results suggest that most knowledge of the Paleotropics concerns a relatively small subset of taxa and comes from relatively few sites, meaning that there are major gaps in the allocation of research effort across the tropics. Furthermore, most research is conducted in protected areas that are atypically large, sufficiently well protected to contain apes, and in countries that rate highly on indices human development, political stability, and safety. This suggests that existing knowledge is not only limited, but it is also biased, potentially painting a dangerously optimistic picture of the state of tropical biodiversity.

A closer examination of work in Southeast Asia highlights these implications. Patterns of research allocation in Southeast Asia ( $n = 55$ ) reflect the general results discussed above: there is a positive relationship between protected area size and research effort and more research is conducted at sites containing orangutans and that are gazetted as National Parks (Figure 4). Each of these effects is independently important, controlling for the effects of the others. On the face of it, the finding that we do most research at sites containing orangutans might seem to be good news from the perspective of this endangered ape. But closer consideration suggests a less positive story, even from the perspective of orangutans. The fact that most information about orangutans is based on sites that are large and well-protected raises concerns about the extent to which we can extrapolate the results of our work to orangutans in other protected areas. Furthermore, more than 75% of orangutans

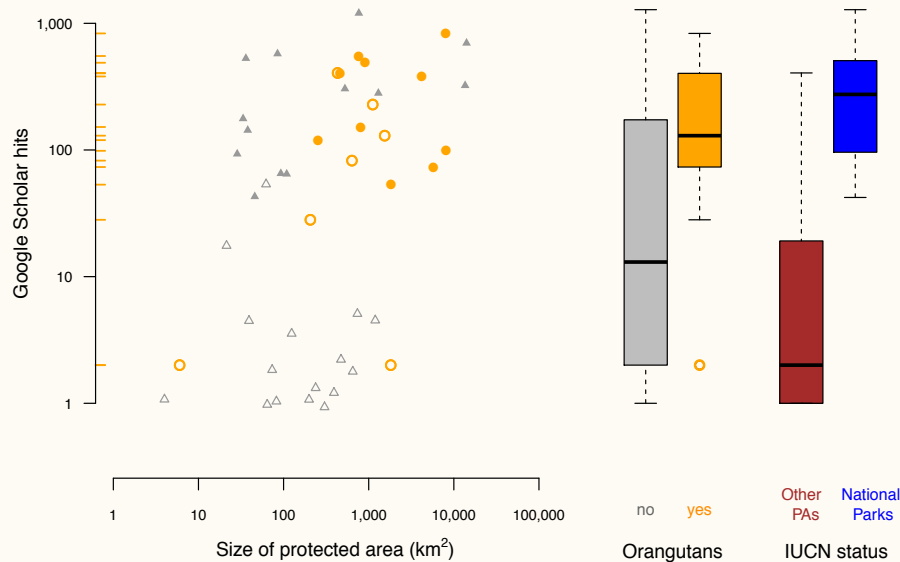


Figure 4. Google Scholar hit counts for all protected areas in Malaysia and Indonesia. Left panel plots Google Scholar hits against protected area size. Solid symbols represent national parks; open symbols represent other protected areas. Gray triangles represent protected areas with no orangutans; orange circles indicate protected areas containing orangutans. Tick marks to the right of the y-axis show hits for all protected areas with orangutans. Boxplots in middle and right panels depict hit counts based on whether or not protected areas contain orangutans (middle panel) and their IUCN protected status (right panel), using the same y-axis as the scatterplot.

live outside formally protected areas (Wich et al., 2008, 2012) under conditions that are typically less conducive to their survival than those found in formally protected forests<sup>12</sup>. Thus, our best empirical data may well be misleading us into thinking that orangutan populations are safer, healthier, and more stable than most actually are. Analysis of the distribution of research effort on orangutans suggests one further implication. The remaining orangutan habitat outside protected areas is becoming increasingly fragmented (Santika et al., 2017), meaning that orangutans in the future will be confined to smaller and smaller patches of forest. As relatively little research is done on orangutans in small forest fragments (e.g., only one protected area containing orangutans is less than 100km<sup>2</sup>, Figure 4), over time our research about orangutans will be less and less applicable to the environments most orangutans inhabit. In other words, because orangutans will increasingly live under conditions we know very little about, our current knowledge will be less useful over time. Many of us want our science to contribute to conservation, but our choices about where to work suggest that much of what we do will have limited applicability. This highlights the need for increased research in marginal habitats, small forest fragments, and outside protected areas (Marshall and Wich, 2016b; Meijaard et al., 2012).

### Recent developments in orangutan research: optimism and caution

Protected areas are critically important for the conservation of tropical biodiversity, including orangutans (Bradshaw et al., 2009, Laurance et al., 2012, Santika et al., 2017; Struebig et al., 2015a). Nevertheless, orangutan conservation efforts focused on protected areas alone are unlikely to be adequate to prevent their extinction.



As noted above, most orangutans live outside protected areas (Wich et al., 2012). In addition, demographic modeling indicates that even if all orangutans living in protected areas were completely safe, these populations are insufficient to ensure long term viability (Marshall et al., 2009a). Although anticipated climate change (Struebig et al., 2015a, 2015b), establishment of new protected areas (Santika et al., 2017), and ongoing losses of orangutans outside protected areas (Meijaard et al. 2011; Voigt et al., 2018) will likely lead to a greater proportion of remaining orangutans being found inside protected areas, it is unlikely that protected areas in the future will support sufficient numbers to guarantee the survival of the species. Thus, forests outside formally protected areas will likely prove to be the difference between orangutan persistence and extinction.

In this context, recent work on orangutans conducted outside protected areas provides some reasons for optimism. For example, intensive surveys of 22 sites across the Berau and East Kutai regencies in East Kalimantan suggest that orangutans can persist at relatively high densities in logged forests, provided they are not hunted (Marshall et al., 2006). Research in Batang Serangan, North Sumatra indicates that orangutans can also survive in mixed agroforest systems via consumption of a mixture of wild and cultivated fruits (Campbell-Smith et al., 2011a, 2011b). Studies in East Kalimantan and Sabah even indicate persistence in industrial-scale oil palm and timber plantations, provided sufficient natural forest is nearby for nesting, seasonal foraging, and thermoregulation (Ancrenaz et al., 2015; Meijaard et al., 2010; Spehar and Rayadin 2017). The authors of these papers are careful to stress that these findings are from relatively short-term studies, suggest much more work is needed, and urge caution in interpreting the results. Although they must be considered preliminary, these results and others indicate that orangutans may be more adaptable and ecologically flexible than was once assumed (Campbell-Smith et al., 2011a, 2011b). This realization has led some orangutan researchers to rethink orangutan biology and the strategies necessary to conserve them (Gregory et al., 2012; Meijaard, 2016; Spehar et al., in press.).

While there is growing acknowledgement of conservation value of lands outside protected areas (Gaveau et al., 2013; Marshall et al., 2006; Meijaard and Sheil, 2008; Meijaard et al., 2012; Struebig et al., 2015a) and undoubtedly a need for new conservation approaches to save orangutans (Marshall et al., 2016b; Meijaard et al., 2012), long-term research suggests reasons to be cautious in our optimism. Orangutans have been studied intensively at many sites across their range, and syntheses of results have uncovered interesting variation that highlights the importance of ecological factors in shaping a wide range of aspects of their basic biology (Delgado and van Schaik, 2000; Wich et al., 2009). Because of differences in geology, soils, plant productivity, and the intensity of El Niño climatic cycles, forests on Borneo (to the east) are generally poorer quality orangutan habitat than those on Sumatra (to the west) (Marshall et al., 2009b; Wich et al., 2011). A similar west to east gradient of declining habitat quality can also be detected within the island of Borneo. Many aspects of orangutan biology vary across this gradient in ways that appear to reflect the fact that they have evolved in environments of different quality that impose distinct levels of extrinsic mortality (summarized in Delgado and van Schaik,



2000 and van Schaik et al., 2009). Moving from west to east, orangutans eat lower quality and more variable diets, exhibit reduced sociality and cultural complexity, and have more robust chewing apparatuses, smaller brains, and faster life histories (Wich et al., 2009). Presumably for these reasons, eastern Bornean orangutans (*Pongo pygmaeus morio*) are more ecologically resilient than their counterparts in western Borneo and Sumatra (Husson et al., 2009). These patterns are fascinating from a biological perspective and have relevance for understanding how orangutans might survive in a changing world.

Most of the optimistic results documenting ecological flexibility and resilience come from research on orangutans in the far eastern part of their range – the populations we would expect to do best under conditions of anthropogenic disturbance due to their evolutionary history. Thus, while these results are intriguing and offer hope for orangutan conservation in the Anthropocene, they may not apply broadly across the entire range of *Pongo*. They may be especially unrepresentative of the far western end of its distribution, which is home to the most threatened and geographically restricted orangutan taxa *P. abelii* and *P. tapanuliensis*. This highlights the importance of long-term research across the range of habitats that orangutans occupy and demonstrates how basic ecological science can help us better interpret results of “more applied” work.

### *Insights from long-term ecological work: examples from Gunung Palung*

Long-term research at single sites can also be highly relevant for conservation. For example, the Cabang Panti Research Station in Gunung Palung National Park, West Kalimantan, Indonesia is an ideal location to study ecological processes that are relevant to conservation. We have a relatively large study area encompassing seven forest types that differ substantially in their elevation, soils, structure, and species composition (Cannon and Leighton, 2004, Marshall, 2010). We have been gathering systematic data on vertebrate population dynamics, plant phenology, and weather across this gradient since the mid 1980s and continuously since 2007. Patterns of plant productivity are quite distinct among forest types (Cannon et al., 2007a; Clink et al., 2017; Dillis et al., 2015), and vertebrate abundances vary greatly in space and time (Allen et al., 2016; Marshall et al., 2014). Here I briefly discuss two simple results from our ongoing work that have important implications for conservation.

### *Source-sink population dynamics*

Gibbon abundance at Cabang Panti differs among forest types by an order of magnitude (Marshall and Leighton, 2006; Marshall, 2010; Figure 5A). During a two-year period of intensive fieldwork my team and I monitored 33 groups of gibbons across the elevational gradient. Territory-specific carrying capacities and numbers of offspring per group were substantially lower in the montane forests than other forest types, suggesting that the uplands are poor quality habitat for gibbons and that they

reproduce at lower rates there (Marshall, 2009, 2010; Figure 5B, C). A resurvey of the montane habitat five years later suggested that the low reproductive rates we observed during our initial sampling were not anomalous. A simple model showed that this demographic structure was highly unlikely if the montane population had

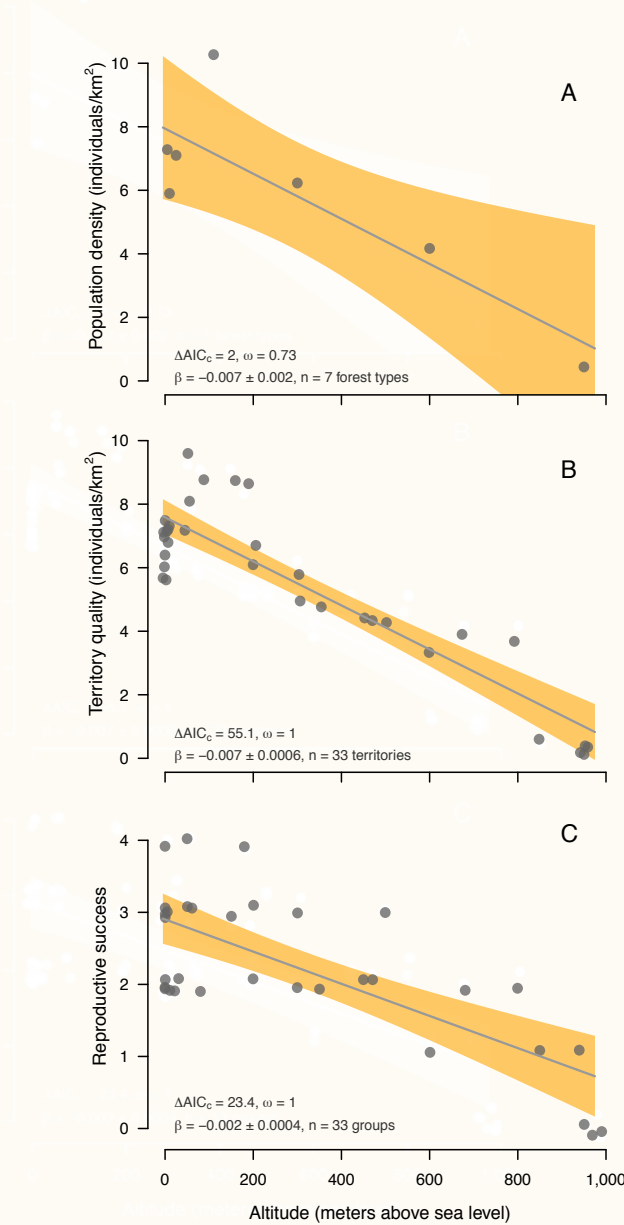


Figure 5. Gibbon population density (individuals/km<sup>2</sup>, A), territory-specific carrying capacity (population density within each territory, B), and an index of reproductive success (C) as a function of altitude. The reproductive success index is the number of offspring observed to have been born in each group between 2000-2007. Data from Marshall (2009). Lines and shaded-regions indicate mean predictions and 95% confidence intervals from ordinary least squares (A, B) or Poisson (C) regressions, respectively. Text in the bottom left of each box provides the  $\Delta AIC_c$  of the bivariate regression ( $y \sim x$ ) compared to an intercept model ( $y \sim 1$ ), the weight ( $\omega$ ) of the bivariate model in a set containing it and the intercept model, the  $\beta$  coefficient ( $\pm$  SE) of the effect of altitude on the dependent variable, and sample size for each regression. To permit distinguishing points on plots, a small amount of random noise was added to the variables in panels B and C (using the jitterO function in base R's plotO command), although models were run on the raw data.

been reproducing at replacement rate, and indicated that population growth rates on top of the mountain were negative (Marshall, 2009). This implied that the montane habitat was a demographic sink, and that the gibbon population found there was only able to persist due to immigration from productive lowland source habitats.

More recent work at Cabang Panti demonstrates that the uplands are low quality for most vertebrates. For example, densities of each of the nine most well sampled vertebrates decline substantially with altitude (Figure 6), and elevation is a strong negative predictor in top models for density of each (Marshall et al., 2014). These

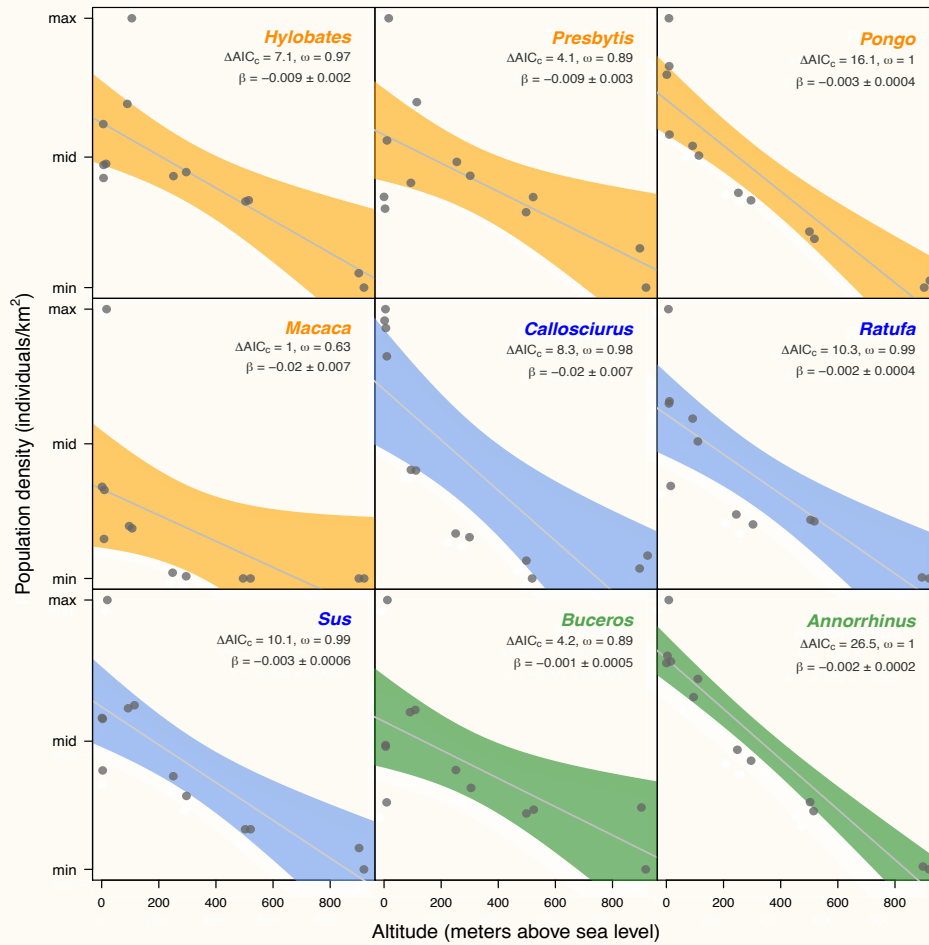


Figure 6. Population density (individuals/km<sup>2</sup>) of the nine most well sampled vertebrate species at the Cabang Panti Research Station as a function of altitude: *Hylobates albibarbis*, *Presbytis rubicunda*, *Pongo pygmaeus*, *Macaca fascicularis*, *Callosciurus prevostii*, *Ratufa affinis*, *Sus barbatus*, *Buceros rhinoceros*, and *Anorrhinus galeritus*. Population density measures have been standardized across taxa to ease comparison, with the y-axis indicating the maximum, minimum, and midpoint of taxon-specific population density. Orange, blue, and green panels indicate primates, non-primate mammals, and birds respectively. Population density measures are averages from October 2007 and February 2013 (data in Marshall et al., 2014). For all panels,  $n = 12$  habitat partitions, where partitions are distinct forest types or the same forest type on two spatially separated ridges (see Marshall et al., 2014). Lines and shaded-regions indicate mean predictions and 95% confidence intervals from ordinary least squares regressions. Text in the top right of each box provides the  $\Delta AIC_c$  of the bivariate regression (density  $\sim$  altitude) compared to an intercept model (density  $\sim 1$ ), the weight ( $\omega$ ) of the bivariate model in a set containing it and the intercept model, and the  $\beta$  coefficient ( $\pm$  SE) of the effect of altitude on population density for each regression.

patterns are consistent with findings elsewhere (e.g., MacKinnon et al., 1996) and support the hypothesis that montane forests are marginal, perhaps sink, habitats for a wide range of mammals and birds. Under this scenario their persistence in upland forests is contingent on the preservation of, and connection to, lowland source forests. As lowland forest is lost across the tropics (e.g., Curran et al., 2004; Gaveau et al., 2014, Margono et al., 2014), an increasing proportion of the remaining ranges of many populations will comprise low quality habitats, resulting in a decrease in the average population density in remaining forest fragments (Marshall, 2009). In extreme cases, loss of lowland source habitat may result in complete extirpation because the only remaining habitat is too poor to support positive population growth rates. Although the quality of montane forests is predicted to improve under most global climate change scenarios (Struebig et al., 2015a, 2015b), it is unclear at what rate this change will occur and to what extent changes in variables used to model species distributions (e.g., temperature, rainfall) will be tracked by the ecological factors that determine density (e.g., food resources, biotic interactions; Blois et al., 2013; Marshall and Wich, 2016b; Wisz et al., 2013). Thus, preservation of source forest and maintenance of contiguity between high and low quality habitats are necessary to ensure persistence of species (Brodie et al., 2015). These results have clear relevance for conservation in fragmented and multi-functional landscapes and highlight the importance of maintaining habitat connectivity.

### *Orangutan population dynamics*

Our vertebrate censuses demonstrate that orangutan population densities at our site vary substantially over both space and time (Marshall et al., 2014). Comparison of orangutan population dispersion as a function of fruit availability reveals complex landscape-level dynamics. Here I highlight one key finding of relevance to conservation, using a subset of our long-term data<sup>13</sup>. Orangutans appear to prefer spending time in the lowland forest types, and their occupancy of the lowlands is well predicted by the percent of plant stems bearing mature or ripe fruits in these forest types (Figs. 7C, D). Occupancy of the peat swamp forests and montane forests is not closely related to the amount of fruit available in those habitats (Figs. 7A, B, E, F, see legend for details). Peaks in abundance in the peat swamp do, however, coincide with periods of relative fruit scarcity in the lowlands – comparisons of models predicting orangutan density in the peat shows that a model using fruit availability in the lowlands is a much better model than one including fruit availability in the peat ( $\omega = 1$ ,  $\Delta AIC_c = 51.8$ ). In the former model, fruit availability in the lowlands is a reliable negative predictor of orangutan abundance in the peat swamps ( $\beta \pm SE = -67 \pm 42$ ). These results indicate that peat swamp forests are “fallback habitats” for orangutans and are important in sustaining populations during periods of fruit scarcity (Cannon et al., 2007b; Marshall et al., 2009c). Work at other sites has demonstrated similar movements across habitat types in response to seasonal variation in fruit availability (Buij et al., 2002; Singleton and van Schaik, 2001). These results may explain why orangutan sites containing a mosaic of forest types consistently support higher densities than more homogenous sites (Husson et al., 2009), and highlight the importance of protecting the full range of habitats that a species occupies.

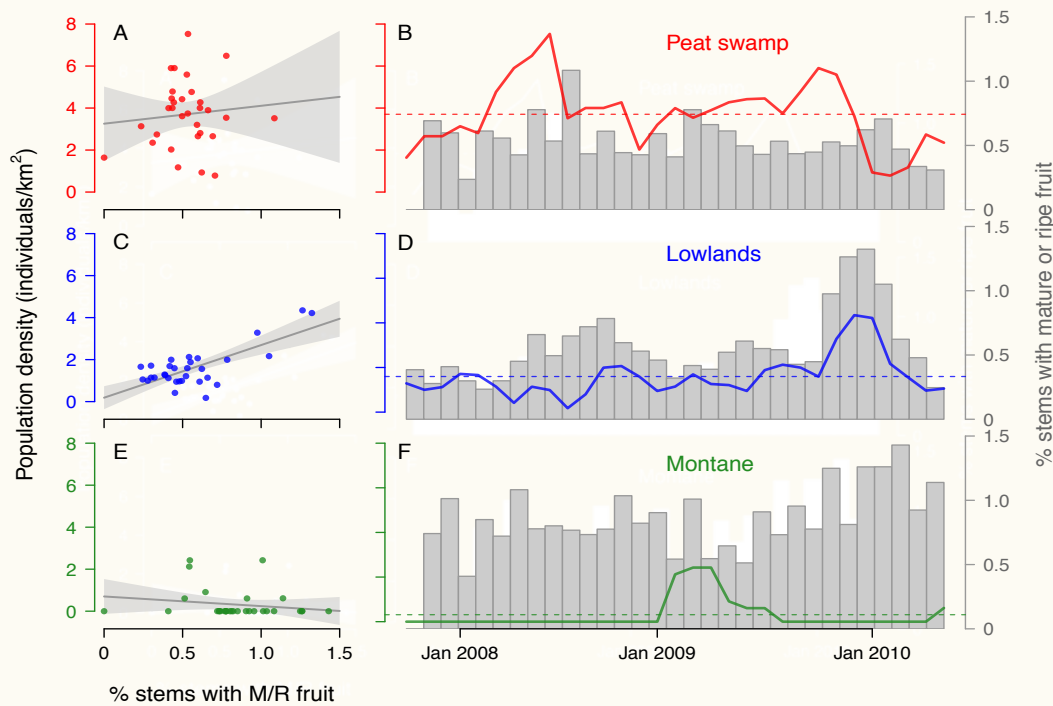


Figure 7. The figures in the left column depict orangutan population density (individuals/km<sup>2</sup>) as a function of the percent of plants with mature or ripe fruit in peat swamp forests (A), lowland forests (here comprising freshwater swamps, alluvial bench, lowland sandstone, lowland granite, and upland granite forests), C) and montane forests (E).

Orangutan occupancy of the lowlands is well explained by fruit availability in those forests—the model of density  $\sim$  fruit availability has model weight ( $\omega$ ) of 1 and  $\Delta AIC_c$  of 21.6 when compared with an intercept model (density  $\sim$  1); the  $\beta$  coefficient ( $\pm$  SE) estimate of the effects of fruit is  $250 \pm 43$ , indicating a reliably positive effect (C). In the peat swamps (A) and montane forests (E) the intercept model is a better model than the fruit model (peat:  $\omega = 0.74$ ,  $\Delta AIC_c = 2.1$ ; montane:  $\omega = 0.67$ ,  $\Delta AIC_c = 1.4$ ) and the  $\beta$  coefficients in the fruit models for the peat and montane forests are not reliable positive predictors (peat:  $85 \pm 155$ ; montane:  $-46 \pm 46$ ; A, E). The figures on the right plot orangutan population density (colored lines, left hand axis is the same as in plots A, C, and E) and the % stems with mature or ripe fruit (gray bars, right hand axis) in peat swamp (B), the lowlands (D), and montane forest (F) over time. Dashed horizontal lines indicate the mean orangutan density in that forest type.

### Occupancy $\neq$ habitat $\neq$ importance

The results from Cabang Panti presented above highlight two simple, related themes regarding to the conservation of species in heterogeneous landscapes. First, we cannot use occupancy as a reliable indicator that an area is viable habitat because vertebrates may occupy places that cannot support them in the long term (e.g., gibbons in montane forests, orangutans in *Acacia* plantations). This indicates that we should be circumspect when drawing conclusions based on relatively short-term studies, especially in environments that we have reason to expect might be poor quality habitats. It also suggests that we should be cautious in our application of occupancy models to conservation. Second, we cannot conclude that a species' absence from a habitat indicates that the area is unimportant for conservation because primates may be absent for extended periods from places that are crucial to their long-term survival (e.g., orangutans in peat swamps). Such a pattern is to be expected in migratory species that depend on places that they occupy only season–

ally, but we are less likely to be alert to the possibility of such dynamics in primates. These themes are likely to become increasingly important as a greater proportion of primate populations inhabit fragments, marginal lands, and heterogeneous landscapes encompassing a mosaic of land uses and different levels of protection. These insights could only have been achieved through long-term research over multiple spatial scales and are examples of how conservation research can directly inform land use planning and permit us to judiciously interpret results from more applied work. Effective ecological science is crucial if we are to align our conservation strategies with Anthropocene realities.

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## End Notes

<sup>1</sup> Neither dependent variable is ideal. The median value is less sensitive to extreme outliers, and therefore provided a better index of overall research investment– but because for 6 of the 23 countries the median number of hits was zero, it did not differentiate among the lower quartile of countries. Thus, I also investigated patterns using mean values. In the mean models I logged the dependent variable to stabilize variance and reduce heteroskedasticity. The median models were negative binomial regressions, the appropriate distribution for dispersed count data.

<sup>2</sup> Total land area in square kilometers, accessed on 1 March 2018 from [https://en.wikipedia.org/wiki/List\\_of\\_countries\\_and\\_dependencies\\_by\\_area](https://en.wikipedia.org/wiki/List_of_countries_and_dependencies_by_area); for Sudan total area was used as total land area was unavailable. I used log(area) as the predictor in my models due to its highly skewed distribution.

<sup>3</sup> Accessed on 1 March 2018 from [https://en.wikipedia.org/wiki/List\\_of\\_countries\\_and\\_dependencies\\_by\\_population](https://en.wikipedia.org/wiki/List_of_countries_and_dependencies_by_population). I used log(population) as the predictor in my models due to its highly skewed distribution.

<sup>4</sup> Population density was calculated directly from population size and area data and log transformed due to its highly skewed distribution.

<sup>5</sup> World Bank's (2016) values, accessed on 28 Feb 2018 from [https://en.wikipedia.org/wiki/List\\_of\\_countries\\_by\\_GDP\\_%28PPP%29\\_per\\_capita](https://en.wikipedia.org/wiki/List_of_countries_by_GDP_%28PPP%29_per_capita)

<sup>6</sup> The Economist's 2017 values, accessed on 1 March 2018 from [http://pages.eiu.com/rs/753-RIQ-438/images/Democracy\\_Index\\_2017.pdf](http://pages.eiu.com/rs/753-RIQ-438/images/Democracy_Index_2017.pdf)

<sup>7</sup> 2015 estimates accessed on 28 Feb 2018 from [https://en.wikipedia.org/wiki/List\\_of\\_countries\\_by\\_Human\\_Development\\_Index](https://en.wikipedia.org/wiki/List_of_countries_by_Human_Development_Index)

<sup>8</sup> Data for 2016 downloaded on 28 Feb 2018 from [www.govindicators.org](http://www.govindicators.org).

<sup>9</sup> Accessed on 28 Feb 2018 from [https://en.wikipedia.org/wiki/List\\_of\\_territorial\\_entities\\_where\\_English\\_is\\_an\\_official\\_language](https://en.wikipedia.org/wiki/List_of_territorial_entities_where_English_is_an_official_language)

<sup>10</sup> GLMs are not linear models in a mathematical sense because they cannot be expressed as a linear combination of their predictors (e.g., as a result of their exponential link functions). Thus, using model weights to create weighted coefficients (as can be done with linear models) is inappropriate (although model averaging can produce averaged predictions in GLMs).

<sup>11</sup> I excluded reviews and any study not conducted on wild apes in their native ranges and based the assessment of whether an area was protected or not based on the location's current listing in World Database of Protected Areas. Data were collected on 12 March 2018.

<sup>12</sup> This proportion is, however, declining due to both heavy orangutan losses outside protected areas and the establishment or enlargement of several protected areas (Santika et al. 2017).

<sup>13</sup> Several collaborators and I are completing a Bayesian occupancy model of our full long-term dataset, which will be published elsewhere.

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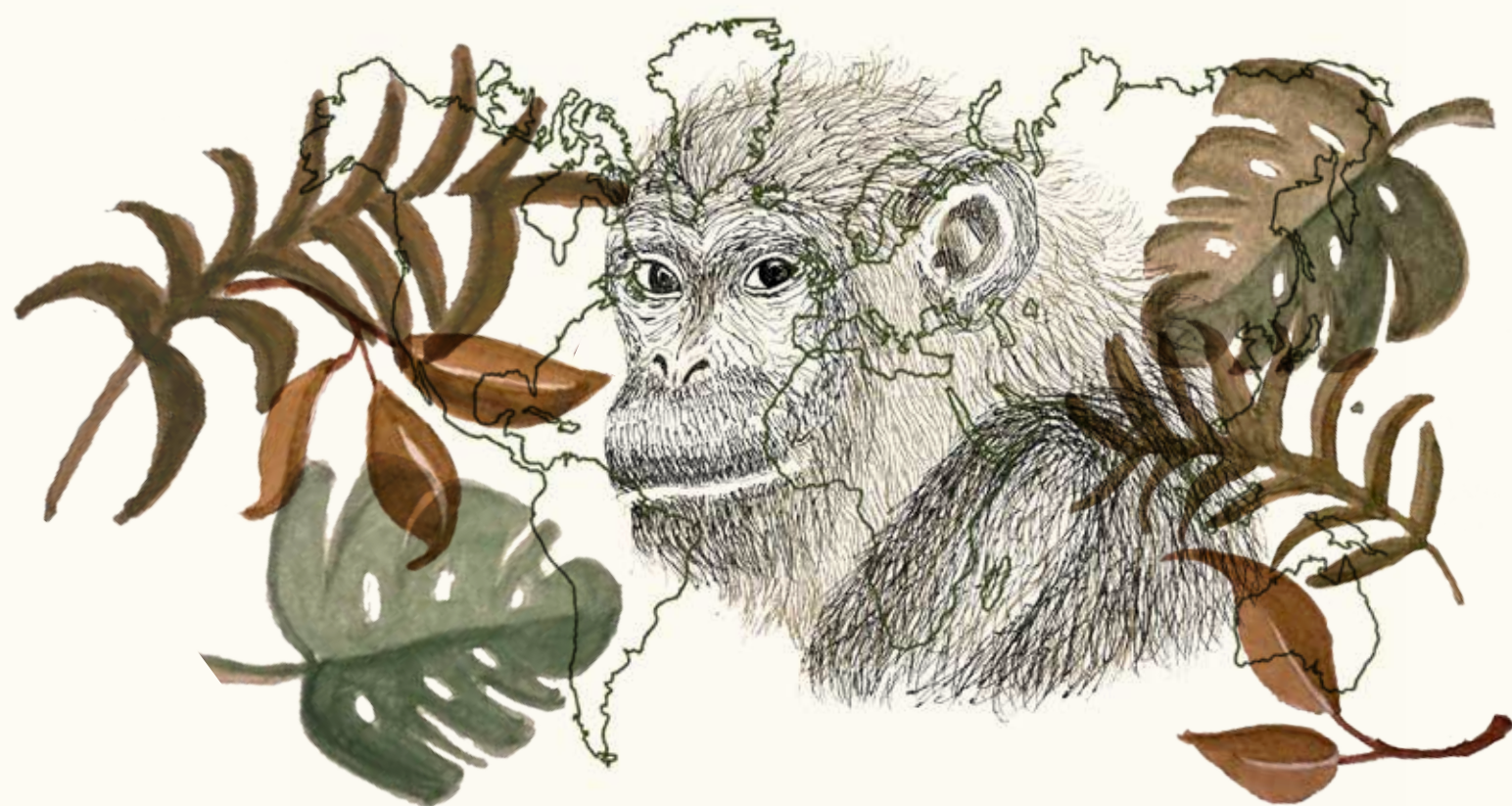
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# Primateology, Biocultural Diversity and Sustainable Development in Tropical Forests

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**Abstract:**

The mismatch between academic conservation science and real-world conservation is well known. Few of us, however, would advocate conservation done in the absence of sound ecological research. I explore this paradox in the context of primate conservation, drawing primarily on recent research in Indonesian Borneo. I use examples at multiple spatial scales to consider how we can maximize the conservation applicability of primatological research in an era of rapid ecological change. I consider the spatial distribution of research effort across protected areas and discuss why it limits the practical relevance of much ecological work. I then discuss why, despite their limitations, long-term ecological studies are vitally important for effective conservation in the tropics. Empirical examples focus on life-history, habitat selection, and source-sink population dynamics in endangered Asian apes.