Global Conservation Significance of Ecuador’s Yasuní National Park

Margot S. Bass1, Matt Finer2, Clinton N. Jenkins3,4, Holger Kreft5, Diego F. Cisneros-Heredia6,7, Shawn F. McCracken8,9, Nigel C. A. Pitman3, Peter H. English10, Kelly Swing7, Gorky Villa1, Anthony Di Fiore11, Christian C. Voigt12, Thomas H. Kunz13

1 Finding Species, Takoma Park, Maryland, United States of America, 2 Save America’s Forests, Washington D. C., United States of America, 3 Nicholas School of the Environment, Duke University, Durham, North Carolina, United States of America, 4 Department of Biology, University of Maryland, College Park, Maryland, United States of America, 5 Division of Biological Sciences, University of California San Diego, La Jolla, California, United States of America, 6 Department of Geography, King’s College London, Strand, London, United Kingdom, 7 College of Biological and Environmental Sciences, Universidad San Francisco de Quito, Quito, Ecuador, 8 Department of Biology, Texas State University, San Marcos, Texas, United States of America, 9 TADPOLE Organization, San Marcos, Texas, United States of America, 10 School of Biological Sciences, University of Texas at Austin, Austin, Texas, United States of America, 11 Department of Anthropology, New York University, New York, New York, United States of America, 12 Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany, 13 Center for Ecology and Conservation Biology, Department of Biology, Boston University, Boston, Massachusetts, United States of America

Abstract

Background: The threats facing Ecuador’s Yasuní National Park are emblematic of those confronting the greater western Amazon, one of the world’s last high-biodiversity wilderness areas. Notably, the country’s second largest untapped oil reserves—called “ITT”—lie beneath an intact, remote section of the park. The conservation significance of Yasuní may weigh heavily in upcoming state-level and international decisions, including whether to develop the oil or invest in alternatives.

Methodology/Principal Findings: We conducted the first comprehensive synthesis of biodiversity data for Yasuní. Mapping amphibian, bird, mammal, and plant distributions, we found eastern Ecuador and northern Peru to be the only regions in South America where species richness centers for all four taxonomic groups overlap. This quadruple richness center has only one viable strict protected area (IUCN levels I–IV): Yasuní. The park covers just 14% of the quadruple richness center’s area, whereas active or proposed oil concessions cover 79%. Using field inventory data, we compared Yasuní’s local (alpha) and landscape (gamma) diversity to other sites, in the western Amazon and globally. These analyses further suggest that Yasuní is among the most biodiverse places on Earth, with apparent world richness records for amphibians, reptiles, bats, and trees. Yasuní also protects a considerable number of threatened species and regional endemics.

Conclusions/Significance: Yasuní has outstanding global conservation significance due to its extraordinary biodiversity and potential to sustain this biodiversity in the long term because of its 1) large size and wilderness character, 2) intact large-vertebrate assemblage, 3) IUCN level-II protection status in a region lacking other strict protected areas, and 4) likelihood of maintaining wet, rainforest conditions while anticipated climate change-induced drought intensifies in the eastern Amazon. However, further oil development in Yasuní jeopardizes its conservation values. These findings form the scientific basis for policy recommendations, including stopping any new oil activities and road construction in Yasuní and creating areas off-limits to large-scale development in adjacent northern Peru.

Introduction

The western Amazon is one of the world’s last high-biodiversity wilderness areas [1,2], a region of extraordinary species richness across taxa [3–9] where large tracts of intact forests remain [10,11]. Indeed, it is still possible to walk continuously through mega-diverse forest from southern Peru to southern Venezuela—a distance of ~2,000 kilometers—without crossing a single road. However, numerous major threats confront the ecosystems of this region—including hydrocarbon and mining projects, illegal logging, oil palm plantations, and large-scale transportation projects under the umbrella of IIRSA (Initiative for the Integration of Regional Infrastructure in South America) [12]. For example, oil and gas concessions now cover vast areas, even overlapping protected areas and titled indigenous lands [13].

* E-mail: matt@saveamericasforests.org
Yasuní National Park (Yasuní) in Ecuador is a major protected area within the western Amazon, yet it faces threats emblematic of those facing the entire region. The park occupies a unique location at the intersection of the Andes (<100 km from the Andean foothills), the Amazon (near the western phytogeographic limit of the Amazon Basin) [14], and the Equator (~1° S) (Figure 1A). Created in 1979, Yasuní covers approximately 9,820 km² [15,16], and is surrounded by a 10 kilometer buffer zone in all directions except to the east, where it meets the Ecuador-Peru border [17].

Yasuní National Park

Figure 1. Ecuador's Yasuní National Park. A) Location of Yasuní National Park at the crossroads of the Amazon, Andes, and the Equator. B) Oil blocks and oil access roads within and surrounding the park. ITT = Ishpingo-Tambococha-Tiputini oil fields, NWC = Napo Wildlife Center, TBS = Tiputini Biodiversity Station, YRS = Yasuní Research Station. The image background is the Blue Marble mosaic of MODIS satellite images. doi:10.1371/journal.pone.0008767.g001

The park overlaps ancestral Waorani (or Huaorani) territory, and is inhabited by at least two clans living in voluntary isolation [16]. In 1989, Yasuní and much of the adjacent area that is now the Waorani Ethnic Reserve were designated a UNESCO Man and the Biosphere Reserve [18]. Yasuní's climate is characterized by warm temperatures (averaging 24–27°C for all months), high rainfall (~3,200 mm annually), and high relative humidity (averaging 80–94% throughout the year) [19]. Yasuní is within the “Core Amazon,” a particularly wet region with high annual rainfall and no severe dry season [20]. The park’s elevational range is small (from ~190 to ~400 m above sea level), but it is crossed by frequent ridges of 25 to 70 meters [21,22]. Soils are mostly geologically young, fluvial sediments from erosion of the Andes [22,23].

Yasuní protects a large tract of the Napo Moist Forests terrestrial ecoregion [24] and the Upper Amazon Piedmont freshwater ecoregion, which contains numerous headwater rivers of the Amazon [25].

Several large-scale development projects exist or have been proposed within the park and its buffer zone. Leased or proposed oil concessions cover the northern half of Yasuní, and four oil access roads have already been built into the park or its buffer zone (Figure 1B). These roads have facilitated colonization, deforestation, fragmentation, and overhunting of large fauna in the northwestern section of the park [26–34] and illegal logging in the south and west [26,35]. Under IIRSA, the Napo River, which borders the northern side of the park, may be dredged in order to become part of a major transport route connecting Brazil’s port of Manaus with Ecuador's Pacific coastal ports [36]. Moreover, large oil palm plantations have been established near the park, just north of the Napo River. Despite these incursions, intact forest still covers the vast majority of Yasuní [32,34].

One of the most serious issues confronting Yasuní is that Ecuador’s second largest untapped oil fields lie beneath the largely intact, northeastern section of the park (in the “ITT” Block, containing the Ishpingo, Tambococha, and Tiputini oil fields; Figure 1B). The adjacent Block 31 contains additional untapped reserves underlying Yasuní. Efforts by scientists and conservationists stopped a new oil-access road into Block 31 planned by Brazil’s Petrobras, but Ecuador could re-auction this block at any time. In response to strong opposition to oil drilling in Yasuní, the Government of Ecuador launched the novel Yasuní-ITT Initiative in 2007. The Initiative offers to keep ITT oil permanently underground and unexploited in exchange for financial compensation from the international community or from carbon markets [37–38]. The Initiative’s primary goals are to respect the territory of indigenous peoples, combat climate change by keeping ~410 M metric tons of CO₂ out of the atmosphere, and protect the park and its biodiversity.

The global conservation significance of Yasuní—a site often referred to anecdotally as one of the most biodiverse places on Earth (e.g., [39,40])—may thus weigh heavily in upcoming state-level and international decisions affecting the park. A preliminary assessment of Yasuní’s biodiversity was conducted in 2004 in response to Petrobras’ planned road [27]. We build upon that effort here and provide the first comprehensive synthesis of biodiversity data for Yasuní, assessing species richness, endemism, and threatened species across various taxonomic groups. We compare our findings to those from other regions, and discuss the global conservation significance of Yasuní by evaluating its potential to sustain a high percentage of Amazonian biodiversity in the long term. We then assess the threats to Yasuní’s
conservation values from oil development. We close with policy recommendations drawing upon these findings.

Results and Discussion

Species Richness

Distribution maps of amphibian, bird, mammal, and vascular plant species across South America (Figure 2) show that Yasuni occupies a unique biogeographic position where species richness of all four taxonomic groups reach diversity maxima (i.e., quadruple richness center, see Figure 3). For amphibians, birds, and mammals, these are not just continental, but global, maxima of species richness at local scales (≤100 km²) [5,41–43]. The same is true of tree community richness (see below). This relatively small (28,025 km²) quadruple richness center encompasses just 0.16% of South America and less than 0.5% of the Amazon Basin. Yasuni is the only strict protected conservation area (considered here as IUCN levels I–IV; see [44,45]) within the quadruple richness center, covering just 14% of its area, while 79% of the center currently coincides with active or proposed oil concessions. In addition to the park, the adjacent Waorani Ethnic Reserve and a disjunct stretch just across the border in northern Loreto, Peru, account for much of the remaining area of the quadruple richness center.

To substantiate the mapping results, we synthesized data sets from field inventories and publications to establish Yasuni’s “local” and “landscape” species richness. The former reflects the complexity of a community, or alpha diversity, while the latter is a measure of the total richness within an area, or gamma diversity, and is a product of the alpha diversity of its local communities and the degree of beta differentiation among them [46]. Local richness is defined here, as it is in the maps for vertebrate taxa (Figure 2A–2C), as the total species occurring in ≤100 km². In the field inventories described below, local richness is typically sampled in areas ranging from a fraction of a hectare to a few hundred hectares. Landscape richness is defined here as the total number of species occurring in areas typically ≤10,000 km² (after Pitman [23]), conveniently roughly equivalent to the size of Yasuni in its entirety. Species richness data qualified as “known,” “documented,” or “confirmed” refer to species actually collected, sighted, or otherwise known by experts to occur within an area. Data qualified as “expected,” “estimated,” or “projected” refer to species anticipated for an area based upon expert opinion or statistical analyses. Due to data limitations, the field inventory analyses focus more on amphibians, reptiles, birds, mammals, and vascular plants, than on fish and insects. We compare Yasuni’s richness to that documented for other sites, in the western Amazon and globally. These comparisons support the mapping results, and suggest that Yasuni is among the world’s most biodiverse sites, both at landscape (Table 1) and local spatial scales (Table 2).
The world's greatest amphibian diversity on a landscape scale is found in the upper Amazon Basin of Ecuador and Peru, and in the Atlantic Forest of eastern Brazil, according to a recent analysis reflecting distribution data and expert opinion (with richness assessed in ~3,000 km² grids) [6]. Data from field inventories support this finding. The 150 amphibian species documented to date throughout Yasuní is a world record among comparable landscapes. Yasuní's known total exceeds the IUCN database total of species known, inferred, and projected to occur in an area of similar size in the greater Iquitos region of northern Loreto, Peru (141 spp./11,310 km²) [47], and exceeds known field records from a much larger area sampled in that region (112 spp./30,150 km²) [48,49]. Yasuní also tops field counts for amphibian diversity from other intensively sampled western Amazon sites: Tambopata in southern Peru (99 spp./1600 km²) [50] and around Leticia, Colombia (123 spp./927 km²) [49,51]. The vast majority of Yasuní’s species are frogs and toads (141 spp.), more than are native to the United States and Canada combined (99 spp.) [47].

At a local spatial scale, the Tiputini Biodiversity Station (TBS; see Figure 1B) currently holds the world record for amphibian alpha diversity (139 documented spp/6.5 km²) [52,53]. This exceeds a recent count from Leticia, Colombia, previously described as having the richest frog assemblage in the world (98 spp./12 km straight line distance) [49,51].

Reptile landscape richness in Yasuní is extremely high as well, with 121 species documented in the park. A smaller area just south of Iquitos is nearly as rich (120 spp./577 km²) [54,55], indicating that high South American reptile landscape richness may extend across the Ecuador-Peru border between Yasuní and Iquitos. Indeed, another count in northern Loreto, Peru exceeds that of Yasuní, although for a much larger area (143 spp./43,425 km² in the greater Iquitos region [49,56]), with sampling throughout this area and slightly beyond (J. R. Dixon, pers. comm). By a considerable margin, Yasuní’s documented landscape richness of reptiles surpasses reports for the southwestern Amazon (Tambopata, Peru: 110 spp./1600 km²) [50] and for all Brazilian Amazon

![Figure 3. Richness center overlap.](https://www.plosone.org/figure3.png)

Richness center overlap of four key focus groups—amphibians, birds, mammals and vascular plants. A richness center is defined as the top 6.4% of grid cells for each taxonomic group (see Materials and Methods for details). 4 groups = area where richness centers for all four groups overlap; 3 groups = richness centers for three groups overlap; 2 groups = richness centers for two groups overlap; 1 group = richness center for just one group occurs; 0 = richness center for none of the four groups.

![Diversity center overlap](https://www.plosone.org/figure4.png)

Diversity center overlap

- 4 groups
- 3 groups
- 2 groups
- 1 group
- Yasuní National Park
- Country boundary
- Quito, Ecuador

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Table 1. Landscape-scale species richness, threatened species, and regional endemics of Yasuni National Park.

| Species          | Species Richness | Threatened Species | Regional Endemics |
|------------------|------------------|--------------------|-------------------|
| Amphibians       | 150              | 1                  | 20                |
| Reptiles         | 121              | 2                  | –                 |
| Birds            | 596              | 2                  | 19                |
| Mammals          | 169–204g         | 8                  | 4                 |
| Fish             | 382–499d         | 0                  | –                 |
| Plants           | 2,704–4,000i     | 28–56f             | ~400–720f         |

*Total species known for Yasuni National Park as a whole (~10,000 km²), from data synthesized for this paper, unless noted.
Lower total represents mammal species known to occur in Yasuni. Higher total is an estimate that includes species known or expected to occur in Yasuni.
Fish species known for Yasuni [68].
Vascular species known for Yasuni (H. Mogollon and J. Guevara, unpub. data, G. Villa, unpub. data, [92–94]).
Vascular plant species expected per 10,000 km² in the global plant diversity center within which Yasuni lies [91].
Total threatened species known to occur in Yasuni, including only those species listed as Critically Endangered, Endangered, or Vulnerable in the IUCN Red List of Threatened Species [47]. Data synthesized for this paper, unless noted.
Lower total represents threatened plant species known to occur in Yasuni. Higher total is an estimate that includes threatened plant species known or expected to occur in Yasuni.
Total regional endemics known to occur in Yasuni, from data synthesized for this paper, unless noted. Dashes indicate unknowns. See text for further description of regional endemics.
Estimated range of total regional endemic plant species that occur in Yasuni. See text for derivation of estimates.

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Yasuni has high fish richness documented in some of its rivers, and may be a global center for fish landscape richness, but worldwide data are still being compiled [64,65]. All of Yasuni’s major rivers ultimately flow into the Napo River in Ecuador or Peru. The Napo River Basin is part of the Upper Amazon Piedmont freshwater ecoregion, which is considered “Globally Outstanding” because experts project its species richness and endemism to be so high [25]. The Napo River Basin has 562 fish species documented [66]. This is more than the 501 species reported for the entire Bolivian Amazon, which contains a potential hotspot of fish biodiversity [67]. The fish diversity for Yasuni includes 382 known species [68], with a total of 499 estimated (K. Swing, unpub. data). The number of known species in Yasuni alone exceeds that of the entire Mississippi River Basin (~375 estimated spp.), one of the three largest watersheds in the world [64]. Just the lower Yasuni River Basin, in the northeast corner of the park within the ITT oil block, has 277 fish species documented [66].

The Tropical Andes contain the greatest resident bird richness on the planet at the landscape scale (as assessed in grids of ~12,000 km²), but the Amazon, including Yasuni, is not far behind [42]. Remarkably, Yasuni as a whole contains at least 596 documented bird species, representing one-third of the Amazon’s total native species (Table 3). At local spatial scales, a north-south stretch of forest in the western Amazon appears to be the richest known globally, whether highland or lowland. Bird lists from individual sites within Yasuni contain between 550 species (in 6.5 km² at TBS) [69] and 571 species (at the 15 km² Napo Wildlife Center) [70]. The only site in the world of a slightly larger, but still comparable, area where documented bird richness rivals that of Yasuni is in the southern Peruvian Amazon, where over 575 species have been found in the 50 km² area around Explorer’s Inn [71]. Similarly, data from standardized field plots (~1 km², and ~15 ha) and mist netting studies indicate that local-scale bird richness within and around Yasuni [72–74] is rivaled only by sites in southeastern Peru [4,69], and exceeds that of sites assessed with similar sampling methods and effort in Bolivia [72], French Guiana [75], Central America [74,76], and other tropical areas globally, including Gabon, New Guinea, and Borneo [72].

For mammals, the Andes and eastern Africa are the richest regions in the world at the landscape scale, according to a recent analysis reflecting species distribution data and expert opinion (assessed in grids of 250,000 km²) [77]. Still, western Amazonian forests, including Yasuni, appear to be globally unique in their ability to support at least 200 coexisting mammal species [5]. Our Yasuni mammal list contains 169 species documented in the park, with at least 35 more expected there based on range data, for a total of 204 species. The Yasuni fauna includes approximately one-third of all Amazonian mammals (Table 3), and 44% of all mammals known from Ecuador (382 spp.) [78]. Considering that Ecuador has the world’s ninth highest mammal diversity [79], finding nearly half of the country’s mammals in a single park is remarkable. At a local scale, the number of coexisting mammal species is also extraordinary. Ten primate species are confirmed to coexist near TBS (A. Di Fiore, unpub. data, [80]), with two additional expected species within the park (Saguinus fuscicollis, reported in the Block 31 oil company environmental impact assessment [81], and Saguinus fuscicollis, which may occur in the northwest portion of Yasuni [78]).

The upper estimate of 12 primate species approaches the richest known sites in the Neotropics (14 sympatric spp. in eastern Peru and western Brazilian Amazon) [82,83] and west Africa [84], and exceeds that for comparably-sized regions of southeast Asia. Importantly, Yasuni’s primate richness represents only one major primate radiation while those in west Africa and southeast Asia represent three different primate radiations.
Table 2. Local-scale species richness of Yasuní National Park.

| Group        | No. of Species | Sample Area | Locale | Source |
|--------------|----------------|-------------|--------|--------|
| Amphibians   | 139            | 6.5 km²     | TBS    | [53]   |
| Reptiles     | 108            | 6.5 km²     | TBS    | [53]   |
| Birds        | 571            | 15 km²      | NWC    | [70]   |
| Birds        | 285            | 1 km²       | TBS    | [74]   |
| Birds        | 284            | 1 km²       | TBS    | [74]   |
| Primates     | 10             | 6.5 km²     | TBS    | [80]   |
| Bats         | 58             | 7.07 km²    | TBS    | [85]   |
| Bats (projected) | >100           | 7.07 km²    | TBS    | [85]   |
| Trees (≥1 cm dbh) | 655 (mean)      | per ha (in 25 ha plot) | YRS    | [96]   |
| Trees (≥10 cm dbh) | 293            | 1 ha        | Capirón| [101]  |
| Trees (≥10 cm dbh) | 282            | 1 ha (in 25 ha plot) | YRS    | R. Condit, pers. comm. |
| Trees (≥10 cm dbh) | 251 (mean)      | per ha (in 25 ha plot) | YRS    | [96]   |
| Trees (≥10 cm dbh) | 242 (mean)      | per ha (n=19) | Within and close to Yasuní | Data taken from [101] |
| Epiphytes    | 313            | 6.5 km²     | TBS    | [93]   |
| Epiphytes    | 146            | 0.1 ha      | TBS    | [93]   |
| Lianas (≥1 cm) | 109            | 1 ha (sampled with non-contiguous transects totalling 0.2 ha) | Yasuní and Waorani Ethnic Reserve | [206] |
| Lianas (≥1 cm) | 98 (mean)       | 1 ha (sampled with non-contiguous transects totalling 0.2 ha (n=6)) | Yasuní and Waorani Ethnic Reserve | [95] |
| Lianas (≥2.5 cm) | 50              | 0.1 ha (sampled in non-contiguous transects, all within 1 ha plot) | Yasuní and Waorani Ethnic Reserve | [95] |
| Lianas (≥2.5 cm dbh) | 27              | 0.1 ha (transect) | YRS    | [92]   |
| Lianas (all dbh size classes) | 96              | 0.2 ha (transect) | YRS    | [92]   |
| Lianas (all dbh size classes) | 65              | 0.1 ha (transect) | YRS    | [92]   |

NWC = Napo Wildlife Center, TBS = Tiputini Biodiversity Station, YRS = Yasuní Research Station. No. of Species represents total species actually documented in the Sample Area through field inventories, unless otherwise noted. Tree and liana data are largely from *terra firme* forests.

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Table 3. Yasuní National Park’s conservation value in terms of protecting Amazonian species.

|          | Yasuní | Amazonia | Amazonian Species in Yasuní (%) |
|----------|--------|----------|---------------------------------|
| Area     | 9,820 km² | 6,683,926 km² | 0.15%                           |
| Amphibians | 150   | 527      | 28%                             |
| Reptiles | 121    | 371      | 33%                             |
| Birds    | 596    | 1,778    | 34%                             |
| Mammals  | 169–204 | 627      | 27–33%                          |
| Fish     | 382–499 | 3,200    | 12–16%                          |
| Plants   | 2,704–4,000 | 40,000 | 7–10%                           |

*Total species known for Yasuní, from data synthesized for this paper, unless otherwise noted in Table 1.

†Unless noted, Amazonia species totals are total estimated native species defined by ecoregions [207], using maps of [208].

‡Estimate from [22], compiled through literature reviews and consultations with experts.

§Fish species expected for the Amazon Basin [209].

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Yasuní has amongst the highest local bat richness for any site in the world [85]. Rigorous comparison of Yasuní’s local richness with that of the Andes and Central America indicates that Yasuní has higher documented and projected richness, and is among the richest of Amazonian sites [85]. Whereas 117 bat species are estimated to occur on a regional scale within the Amazon Basin [86], Yasuní is projected to harbor comparable richness on just a local scale [85]. Using the same protocol and effort, ten plots of 1 ha were sampled at Yasuní’s Tiputini Biodiversity Station (TBS), at Bombuscaro River in Podocarpus National Park in Ecuador’s Andes, and at La Selva in Costa Rica. (La Selva was included in the study because its bat assemblage is so well studied that it could be used to assess the accuracy of different estimation methods.) In the sample plots, documented phyllostomid species were highest in Yasuní by a statistically significant margin (TBS = 44 spp., La Selva = 31 spp., Podocarpus = 22 spp.) [85]. Using a statistical tool—Jackknife 2—to estimate total richness from the field data, phyllostomid richness was projected to be highest at TBS (TBS = 58 spp., La Selva = 39 spp., Podocarpu = 25 spp.). Rarefaction of capture data from TBS and La Selva to the number of individuals captured at Podocarpus showed that both sites were statistically richer than Podocarpus (TBS = 37±4.8 spp., La Selva = 27±3.6 spp.). Rarefaction of capture data from TBS to the number of individuals captured at La Selva showed TBS to be the richest of the three (TBS = 44±1.1 spp.). Capture data at TBS represented only 64% of the projected total richness. While Jackknife 2 was considered the best of the tested estimators, its projection of La Selva’s phyllostomid richness was ~20% lower than the known total. Assuming that Jackknife 2 underestimated phyllostomid richness at the other sites to the same degree (i.e., ~20% underestimate), and given the typical proportion of phyllostomids within Neotropical rainforest bat assemblages, Neotropical rainforest bat assemblages,
overall bat species richness for TBS was projected to be >100 coexisting species. This was nearly double the total projected for Podocarpus (>50 spp.) [85], and considerably more than La Selva’s documented total (74 spp.) [87]. Furthermore, TBS has significantly higher diversity than the Andes or Costa Rica, as measured by both the Shannon-Weiner and Simpson diversity indices. Indeed, TBS has the highest Shannon-Weiner diversity index for any bat assemblage in the world (H’ = 3.04) [95], exceeding the global record from a savanna ecosystem in Bolivia (H’ = 2.58) [88].

For insects, global data are preliminary, but Yasuni appears to harbor extremely rich ant [40,89] and beetle [7] assemblages. A single hectare of forest in Yasuni is projected to contain at least 100,000 insect species (T. Erwin, pers. comm.), approximately the same number of insect species as is found throughout all of North America [90]. This comparison illustrates again how extremely diverse Yasuni is at local scales. The Yasuni per-hectare insect estimate represents the highest estimated biodiversity per unit area in the world for any taxonomic group (T. Erwin, pers. comm.).

For vascular plants, Yasuni is among the richest areas globally at a landscape scale. Yasuni falls within one of only nine centers of global plant diversity, defined in a recent assessment as those areas having more than 4,000 estimated vascular plant species per 10,000 km² [91]. Yasuni is not, however, in the top five richest centers (Costa Rica-Chocó, Atlantic Brazil, Tropical Eastern Andes, Northern Borneo, and New Guinea, each with more than 5,000 estimated spp./10,000 km²) [91]. Field inventory data lag behind that assessment, with just over 2,700 vascular plant species currently documented for Yasuni: 138 lianas [92], 313 epiphytes [93], 140 pteridophytes [94], and 2,113 trees and shrubs—with 1,813 identified (H. Mogollon and J. Guevara, unpub. data) and another 300 unidentified but morphologically distinct (G. Villa, unpub. data). Yasuni’s total richness of vascular plants climbs to at least 3,213 with expected species, including 161 additional trees and shrubs collected from provinces bordering Yasuni (H. Mogollon and J. Guevara, unpub. data) and 486 lianas collected either in Yasuni or in the Waorani Ethnic Reserve [95].

At the local scale, Yasuni does appear to protect the richest area in the world of woody plant species. Yasuni holds at least four global records for documented tree and liana richness: mean number of tree and shrub species per ha (size classes ≥1 cm dbh, per 25–50 ha plot sampled) [96]; mean number of larger tree species per ha (size classes ≥10 cm dbh, per 25–50 ha plot sampled) (Tables 2 and 4, and [96]); liana species ≥2.5 cm in comparable 0.1 ha plots [92]; and liana species of all size classes in 0.1 ha plots [92]. Yasuni also holds a projected global record for tree and shrub species richness, from the Center for Tropical Forest Science (CTFS) Yasuni plot. With over 1,100 species-level taxa of trees and shrubs documented in the first 25 hectares of Yasuni’s CTFS plot [96], census of the remaining 25 hectares is projected to bring the total to over 1,300 species (≥1 cm dbh) [97]. This would make it by far the richest CTFS 50 ha plot yet sampled in the world (Table 4). Yasuni also holds three world records in diversity measures for woody plant species. The Yasuni CTFS plot has the highest average diversity of trees and shrubs per ha, as measured by both the Shannon-Weiner and the Fisher’s alpha diversity indices, and per 25 ha, as measured by the Fisher’s alpha diversity index (with the Shannon-Weiner not available for 25 hectares across plots) (see Table 4, references therein, and [98]). At the local scale, Yasuni also holds the global lowland forest record for documented epiphytes in 0.1 ha, surpassing even some Andean counts [93]. Together, these studies suggest that a typical hectare of terra firme forest in Yasuni contains upwards of 655 tree species [96]—more than are native to the continental United States and Canada combined [99]—and well over 900 total species of vascular plants [92,93,95,96].

The forests harboring record-setting global woody plant species richness are not restricted to Yasuni alone. While plots sampling trees and shrubs down to 1 cm dbh have not been established throughout the Amazon Basin, plots for larger trees have (≥10 cm dbh) [9,23,100,101]. These confirm that the world’s richest 1 ha tree plots occur in Amazonia, and that Amazonia’s richest plots occupy a large east-west band of forest stretching along the equator from Yasuni to Manaus, 1,700 kilometers to the east [9,100,101]. Thus, the richness in tree species found in Yasuni does not extend north-south throughout all western Amazonian forests [23]. It is still too early to determine which areas of this equatorial band have the most diverse tree communities at the 1 ha scale. To date, Yasuni and forests within 200 kilometers of Yasuni boast the fifth, sixth, and seventh most diverse 1 ha tree plots of the more than one hundred established in this equatorial band (Cayabeno = 307 spp. [102], Boca Curaray = 308 spp. [101], Capiron = 293 spp.) [N. Pitman, unpub. data, [101], exceeding all previous counts published as world records [103]. Even when compared to Malaysian forests, the richness of this narrow east-west band of Amazonian forests is apparently unmatched [104].

As can be seen from the above field data, sample areas and effort are generally not standardized throughout the tropics. We sought to address this uncertainty in three ways. First, we distinguished between “documented” species totals—i.e., where identifications have been confirmed by us or other experts and thus we consider them to have minimal error—and “estimated” totals—i.e., where richness numbers may be higher, but uncertainty is greater. Second, given that area has a major effect on total richness [46,98], and that diversity in its strict sense is appropriately measured as the number of species in a sample of standard size [46], we divided our richness analyses into two area-based scales, local and landscape richness (after Whitaker [46] and Pitman et al. [23]). Third, we consistently noted the size of sampled areas from which richness records are drawn. When studies did not give the size, we made our own rough calculations [49]. The reader is thus alerted to any comparisons between unequal areas, providing transparency about, but not minimizing, the uncertainty of comparisons within the two area-based scales of analysis. In light of our precautions, we consider the field analyses and conclusions to be as reliable and conservative as possible (see Text S1 for more details on uncertainty in the data). With regard to the extent and boundaries of the quadruple richness center, we also must acknowledge the uneven sampling across Amazonia [5,100,105,106]. Yet the most standardized and therefore definitive field inventory comparisons of Yasuni’s local richness with other sites are those for trees and shrubs (Table 4, [23,98,100,101]), birds [72–75], and bats [85]. For all these taxa, Yasuni’s known or expected richness is among the highest in the world. Thus, while the boundaries and full extent of the quadruple richness center may change, the field data substantiate its general location.

**Conclusions on Yasuni’s Species Richness**

Yasuni National Park is globally outstanding for its exceptional biological richness on both landscape and local scales, across taxonomic groups. On a landscape scale, the area is one of the two richest in the world for amphibian species, the second richest known to date for reptiles, within the top nine richest centers for vascular plants (and the top center for trees and shrubs), among the richest lowland areas for birds, high in mammal richness (particularly for bats), and very rich in fish species. At the local scale, species distribution maps (Figure 2) are substantiated by
Therefore, even within the western Amazon, Yasuní stands out. Uniformly north-south along the Andean foothills (Figures 2A–2D), species richness of different taxonomic groups does not extend to the park's high documented areas for birds; and the projected globally richest tree communities; a stretch of one of the globally richest documented reptile and combined herpetofaunal mammal communities. Field data further suggest that Yasuní protects the forests harboring peak global richness for amphibians, birds, and mammals. Field data further suggest that Yasuní protects the globally richest documented reptile and combined herpetofaunal communities; a large stretch of forest with the globally richest documented tree communities; a stretch of one of the globally richest documented areas for birds; and the projected globally richest bat and insect communities. Notably, the park's high species richness of different taxonomic groups does not extend uniformly north-south along the Andean foothills (Figures 2A–2D). Therefore, even within the western Amazon, Yasuní stands out.

The high landscape-scale diversity described in the Andes for some taxa is due in large part to its greater environmental heterogeneity or "geodiversity" [91]. For example, the Ecuadorian Tropical Andes have higher landscape-level plant (see Figure 2D), bird [42], and mammal diversity [77], but Yasuní is clearly richer at local scales for these three groups. At the coarse scales of analysis used in these and similar studies, typically around 10,000 km², individual cells of analysis in the Andes can encompass a wide variety of habitats and environmental conditions (or even multiple mountain ranges). The consequence is to inflate the richness values well above what one would ever find at a single location on the ground. While such large biogeographic areas may indeed have the high richness numbers reported, it is unlikely that any single site within them approaches such high numbers. In Yasuní, that is not the case, as illustrated in Figure 2 by the high species richness within the finer resolution grid cells (100 km²) of the three animal groups—amphibians, birds, and mammals.

It is still unknown exactly why Yasuní is so diverse. Richness is likely fostered by the conditions found at this unique location at the intersection of the Andes, the Amazon, and the Equator. Pitman et al. [23] have speculated that the most important factors behind Yasuní's high plant diversity are the high rainfall and relatively aseasonal climate. This hypothesis is consistent with global-scale diversity trends and climate-richness relationships documented for plants and other groups of organisms (e.g., [107,108]). High annual rainfall coupled with a limited dry season appears to be a major factor for the high amphibian diversity as well [41]. Average annual rainfall in Yasuní (~3,200 mm) is considerably higher than the average across Amazonia (~2,400 mm) [109]. Moreover, unlike the southwestern Amazon, temperatures in Yasuní never fall below the critical plant-chilling-damage temperature of 10°C [19,110]. This combination of ever-wet and ever-warm conditions is due to Yasuní’s being at a geographic crossroads—in close proximity to both the equator and the Andes [93]. Separately, Kraft et al. [111] found that ecological “strategy differentiation” among species is another major factor in the maintenance of Yasuní’s high tree diversity. Its aseasonality, resulting in year-round availability of fruit and flowers, may be an important factor in the park’s exceptional number of coexisting birds [112] and mammals [5] and overall high animal biomass. Other potential factors abound, such as possible climatic stability over evolutionary time-scales [113], but well-supported explanations for the region’s diversity are still elusive.

### Threatened Species

Yasuní is home to a considerable number of globally threatened species, i.e., those listed by the IUCN as Critically Endangered, Endangered, or Vulnerable [47] (Tables 1, 5, 6, 7). These include 13 documented vertebrate species and an estimated 56 plant species (28 documented in the park, with another 28 expected). An additional 15 vertebrate species are Near Threatened, along with an estimated 47 plant species (30 documented, 17 expected). The tree Rollinia helosioides is the only Critically Endangered species (i.e., facing an extremely high risk of extinction in the wild).

| Site                           | Country  | Area (ha) | Tree Spp. (≥ 1 cm dbh, Mean/ha) | Tree Spp. (≥10 cm dbh, Mean/ha) | Tree Spp. (≥1 cm dbh, Total) | Fisher’s alpha (Trees ≥1 cm dbh, Mean/ha) | Total Census Area (ha) | Source |
|-------------------------------|----------|-----------|---------------------------------|----------------------------------|-------------------------------|--------------------------------------------|------------------------|--------|
| Yasuní National Park          | Ecuador  | 1104      | 187.1                           | 25                               |                               |                                            |                        | [96]   |
| Lambir Hills National Park    | Malaysia | 1853      | 165.3                           | 52                               |                               |                                            |                        | [104]  |
| Pasoh Forest Reserve          | Malaysia | 814       | 123.9                           | 50                               |                               |                                            |                        | [210]  |
| Khao Chong Wildlife Refuge    | Thailand | 612       | –                               | 24                               |                               |                                            |                        | [211]  |
| Yunnan Province (Xishuangbanna) | China    | 468       | –                               | 20                               |                               |                                            |                        | [211]  |
| Bukit Timah Nature Reserve    | Singapore| 113       | 60.0                            | 2                                |                               |                                            |                        | [212]  |
| Korup National Park           | Cameroon | 494       | 48.0                            | 50                               |                               |                                            |                        | [213]  |
| Palanan Wilderness Area        | Philippines| 335      | 43.4                            | 16                               |                               |                                            |                        | [214]  |
| Barro Colorado Island         | Panama   | 301       | 34.6                            | 50                               |                               |                                            |                        | [215]  |
| Okapi Faunal Reserve (Ituri)  | D.R. Congo| 57        | 29.5                            | 40                               |                               |                                            |                        | [216]  |
| La Planada Nature Reserve     | Colombia | 228       | 30.6                            | 25                               |                               |                                            |                        | [217]  |
| Sinharaja World Heritage Site | Sri Lanka| 205       | 24.4                            | 25                               |                               |                                            |                        | [218]  |
| Doi Inthanon National Park    | Thailand | 162       | 19                              | 15                               |                               |                                            |                        | [219]  |
| Ken-Ting National Park        | Taiwan   | 125       | –                               | 3                                |                               |                                            |                        | [220]  |
| Huai Kha Khaeng W. Sanctuary  | Thailand | 251       | 23.3                            | 50                               |                               |                                            |                        | [221]  |
| Luquillo Experimental Forest  | Puerto Rico| 138      | –                               | 16                               |                               |                                            |                        | [222]  |
| Northern Taiwan (Fushan)      | Taiwan   | 110       | –                               | 25                               |                               |                                            |                        | [221]  |
| Mudumalai Wildlife Sanctuary  | India    | 71        | 5.9                             | 50                               |                               |                                            |                        | [223]  |

Table 4. Global comparison of shrub and tree species richness in the Center for Tropical Forest Science (CTFS) Forest Dynamics Plots.
documented in Yasuni (Table 7). Of other plant species documented or expected in Yasuni, seven are Endangered (i.e., facing a very high risk of extinction in the wild). Among these is Cedrela fissilis, a tree targeted by illegal loggers. Most of its natural subpopulations within Ecuador have already been destroyed [114].

Eight of the threatened vertebrates are mammals, which likely qualifies Yasuni as a threatened mammals hotspot (defined by Ceballos et al. [43] as being the top 5% of 10,000-km² cells in a global grid). Yasuni has important populations of two globally Endangered mammal species, the White-bellied Spider Monkey (Ateles belzebuth) and the Giant Otter (Pteronura brasiliensis). The White-bellied Spider Monkey was uplisted from Vulnerable to Endangered in 2008 because it is thought to have declined by at least 50% over the past 45 years (three generations), largely due to over-hunting and habitat loss [115]. Similarly, the Giant Otter may experience a halving of population size over the next 20 years due to accelerating habitat destruction and degradation [116].

Yasuni and the Pastaza River are the Giant Otter’s most important refuges in Ecuador [117]. Fewer than 250 sexually reproductive individuals are estimated to remain in-country, with

| IUCN Category | Amphibians | Reptiles | Birds | Mammals | Plants | Total |
|---------------|------------|----------|-------|---------|--------|-------|
| Critically Endangered (CR) | – | – | – | 1 | 1 |
| Endangered (EN) | – | – | 2 | 4 | 6 |
| Vulnerable (VU) | 1 | 2 | 2 | 6 | 23 |
| Near Threatened (NT) | 1 | – | 5 | 9 | 30 |
| **Total** | 2 | 2 | 7 | 17 | 58 |

Table 5. Threatened and Near Threatened species totals for Yasuni National Park.

Table 6. Threatened and Near Threatened vertebrates known to occur in Yasuni National Park.

| Class | Family | Species | Common Name | IUCN |
|-------|--------|---------|-------------|------|
| Amphibians | Bufonidae | Atelopus spumarius (complex) | Pebas Stubfoot Toad | VU |
| Reptiles | Podocnemididae | Podocnemis unifilis | Yellow-spotted River Turtle | VU |
| Birds | Psittacidae | Ara militaris | Military Macaw | VU |
| | Parulidae | Dendroica cerulea | Cerulean Warbler | VU |
| | Anatidae | Neochen jubata | Orinoco Goose | NT |
| | Accipitridae | Harpa harpyja | Harpy Eagle | NT |
| | Accipitridae | Morphys guianensis | Crested Eagle | NT |
| | Furnariidae | Synallaxis cherriei | Chestnut-throated Spinetail | NT |
| | Thamnophilidae | Thamnophilus praecox | Cocha Antshrike | NT |
| Mammals | Mustelidae | Pteronura brasiliensis | Giant Otter | EN |
| | Atelidae | Ateles belzebuth | White-bellied Spider Monkey | EN |
| | Trichechidae | Trichechus inunguis | Amazonian Manatee | VU |
| | Tapiridae | Tapirus terrestris | Lowland Tapir | VU |
| | Dasyopodidae | Priodontes maximus | Giant Armadillo | VU |
| | Atelidae | Lagothrix poeppigii | Poeppig’s Woolly Monkey | VU |
| | Felidae | Leopardus tigrinus | Oncilla | VU |
| | Phyllostomidae | Vampyressa melissa | Melissa’s Yellow-eared Bat | VU |
| | Callitrichidae | Saginus tripartitus | Golden-mantled Tamarin | NT |
| | Felidae | Leopardus wiedii | Margay | NT |
| | Canidae | Atelocynus microtis | Short-eared Dog | NT |
| | Canidae | Speothos venaticus | Bush Dog | NT |
| | Myrmecophagidae | Myrmecophaga tridactyla | Giant Anteater | NT |
| | Tayassuidae | Tayassu pecari | White-lipped Peccary | NT |
| | Phyllostomidae | Vampyrum spectrum | Spectral Bat | NT |
| | Phyllostomidae | Stumira aporaphilum | Tschudi’s Yellow-shouldered Bat | NT |

Listings in the IUCN column are from the IUCN Red List of Threatened Species [47]. Abbreviations: EN = Endangered (facing a very high risk of extinction in the wild), VU = Vulnerable (facing a high risk of extinction in the wild), and NT = Near Threatened (close to qualifying for or is likely to qualify for a threatened category in the near future).
Table 7. Threatened plant species known to occur in Yasuní National Park.

| Family                  | Species                     | Common Names            | Habit                    | IUCN   |
|-------------------------|-----------------------------|-------------------------|--------------------------|--------|
| Annonaceae              | Rollinia helosioides        | –                       | Tree                     | CR     |
| Apocynaceae             | Aspidosperma darianense     | –                       | Tree                     | EN     |
| Meliaceae               | Cedrela fissilis            | Missionaries' Cedar     | Tree                     | EN     |
| Meliaceae               | Trichilia elae             | –                       | Tree                     | EN     |
| Myristicaceae           | Virola surinamensis        | Baboonwood              | Tree                     | EN     |
| Alismataceae            | Echinodorus eglandulosus    | –                       | Aquatic Herb             | VU     |
| Annonaceae              | Cremastosperma megalophyllum| –                       | Tree                     | VU     |
| Asteraceae              | Citronia eggersii          | –                       | Liana                    | VU     |
| Begoniaceae             | Begonia oelligardi         | –                       | Terrestrial Herb         | VU     |
| Begoniaceae             | Begonia sparreana          | –                       | Terrestrial Herb         | VU     |
| Meliaceae               | Cedrela odorata            | Cigar-box Wood, Red Cedar| Tree                     | VU     |
| Meliaceae               | Trichilia saltidinis       | –                       | Tree                     | VU     |
| Proteaceae              | Euplassa occidentalis      | –                       | Tree                     | VU     |
| Rubiaceae               | Palicourea ananguana       | –                       | Shrub, Small Tree        | VU     |
| Rubiaceae               | Simira wurdackii           | –                       | Tree                     | VU     |
| Sapotaceae              | Micropholis brochidodroma  | –                       | Tree                     | VU     |
| Sapotaceae              | Pouteria gracilis          | –                       | Tree                     | VU     |
| Sapotaceae              | Pouteria nudipetala        | –                       | Tree                     | VU     |
| Sapotaceae              | Pouteria pubescens         | –                       | Tree                     | VU     |
| Sapotaceae              | Pouteria vernicosa         | –                       | Tree                     | VU     |
| Annonaceae              | Rollinia dolichopetala     | –                       | Tree                     | NT     |
| Annonaceae              | Rollinia eucadorensis      | –                       | Tree                     | NT     |
| Annonaceae              | Tetrameranthus globuliferus| –                       | Tree                     | NT     |
| Annonaceae              | Trigynaea triplinervis     | –                       | Tree                     | NT     |
| Cecropiaceae            | Pourouma petialulata       | –                       | Tree                     | NT     |
| Chrysobalanaceae        | Licania velutina           | –                       | Tree                     | NT     |
| Fabaceae s.l.           | Inga sarayacensis         | –                       | Tree                     | NT     |
| Fabaceae s.l.           | Senna trolliiiflora        | –                       | Tree                     | NT     |
| Gesneriaceae            | Besleria quadrangulata     | –                       | Subfructescent Herb      | NT     |
| Gesneriaceae            | Nautilocalyx ecuadoranus   | –                       | Terrestrial Herb         | NT     |
| Gesneriaceae            | Pearcea hypocrystiflora    | –                       | Terrestrial Herb         | NT     |
| Lauraceae               | Nectandra microcarpa       | –                       | Tree                     | LR/nt  |
| Loranthaceae            | Psittacanthus barlowii     | –                       | Parasitic Shrub          | NT     |
| Marantaceae             | Calathea paucifolia       | –                       | Terrestrial Herb         | NT     |
| Marantaceae             | Calathea plurisipicata    | –                       | Terrestrial Herb         | NT     |
| Marantaceae             | Calathea vetchiana        | –                       | Terrestrial Herb         | NT     |
| Melastomataceae         | Cidemia longipedunculata   | –                       | Shrub, Small Tree        | NT     |
| Melastomataceae         | Miconia abbreviata        | –                       | Small Tree               | LR/nt  |
| Melastomataceae         | Miconia lugonis           | –                       | Tree                     | NT     |
| Memecylaceae            | Mouriri laxiflora         | –                       | Tree                     | NT     |
| Olacaceae               | Minquartia guianensis     | Black Manwood           | Tree                     | LR/nt  |
| Rubiaceae               | Alseis lugonis            | –                       | Tree                     | NT     |
Yasuni harboring an estimated 20 groups, each consisting of a reproductive pair and averaging five individuals (V. Uteras, unpub. data in [27,117]).

Yasuni is also home to numerous globally Vulnerable species (i.e., facing a high risk of extinction in the wild), including six more mammals. Poeppig’s Woolly Monkey (Lagothrix poeppigii), Lowland Tapir (Tapirus terrestris), and Giant Armadillo (Priodontes maximus) are believed to have experienced population declines of at least 30% over the past three generations (45 years) due primarily to hunting and habitat loss [118–120]. Similar declines are forecast over the next several generations for the Amazonian Manatee (Trichechus inunguis) and Crested Eagle (Morphnus guianensis) that is also Near Threatened. Bush Dogs and Jaguars have been documented at TBS with camera traps (K. Swing, pers. comm.). In sum, Yasuni protects a considerable number of threatened species, and is likely a global hotspot for threatened mammals.

**Endemism**

Assessing endemism in the western Amazon continues to be a major challenge. Vast areas have yet to be surveyed by scientists, and in consequence many species distributions are poorly known [100,105,134]. At present, better information appears to be available for amphibians and birds than for other groups. Although not generally viewed as protecting part of a region with globally outstanding endemism, Yasuni does in fact harbor a considerable number of regional endemics. It has 43 documented vertebrates and an estimated 220–720 plants (Table 1) that are regional endemics, defined here as species completely, or mostly, confined to the Napo Moist Forests ecoregion [135]. This 251,700 km² area forms the northwestern part of the Napo area of endemism, one of eight such areas posited for the Amazon [136].

Yasuni is home to 20 amphibian species that are endemic to the Napo Moist Forests (Table 8), including two *Pristimantis* species endemic to the park. This number may rise, as 15 species discovered at TBS are new to science [53]. An additional 21 species have the vast majority of their ranges within the Napo Moist Forests, including the Near Threatened *Rhinella festae*. Duellman [137] indicated that the upper Amazon Basin in Ecuador and Peru is notable for its high amphibian endemism.

### Table 7. Cont.

| Family       | Species               | Common Names          | Habitat     | IUCN   |
|--------------|-----------------------|-----------------------|-------------|--------|
| Rubiaceae    | Coussarea cephaloidea | –                     | Shrub, Small Tree | NT     |
| Rubiaceae    | Coussarea dulcifolia  | –                     | Shrub, Small Tree | NT     |
| Rubiaceae    | Coussarea spicifloris | –                     | Shrub, Small Tree | NT     |
| Santalaceae  | Acanthosyris amnonagustata | –                 | Tree       | NT     |
| Sapotaceae   | Pouteria platypylla   | –                     | Tree       | LR/nt  |
| Sapotaceae   | Pradosa atrovilaceae  | –                     | Tree       | LR/nt  |
| Tillaceae    | Pentaplasis huaraonara | –                     | Large Tree  | NT     |
| Ulmaceae     | Ampelocera longissima | –                     | Tree       | NT     |

Listings in the IUCN column are from the IUCN Red List of Threatened Species [47]. Abbreviations: CR = (facing an extremely high risk of extinction in the wild), EN = Endangered (facing a very high risk of extinction in the wild), VU = Vulnerable (facing a high risk of extinction in the wild), and LR/nt or NT = Near Threatened (close to qualifying for or is likely to qualify for a threatened category in the near future). doi:10.1371/journal.pone.0008767.t007
Yasuni lies within the Upper Amazon-Napo lowlands Endemic Bird Area [130]. Six of the ten range-restricted birds listed for this Endemic Bird Area are confirmed for Yasuni, including the Near Threatened Cocha Antshrike (Thamnophilus praecox). Ridgely and Greenfield [129] consider an additional 16 bird species to be endemic to eastern Ecuador and adjacent northeastern Peru, of which 13 are confirmed for Yasuni. Thus, at least 19 regionally endemic birds inhabit the park (Table 8).

At least four mammal species within Yasuni are endemic to the Napo Moist Forests ecoregion (Table 8). Two of them—Yasuni’s Round-eared Bat (Lophostoma yasuni) and Streaked Dwarf Porcupine (Sphiggurus ichillus)—are endemic to the Ecuadorian Amazon [78]. In fact, the only known specimen of L. yasuni was collected inside the park [78,139]. The Golden-mantled Tamarin and Equatorial Saki (Pithecia aequatorialis) cross over into Peru, but appear to be restricted to the Napo Moist Forests ecoregion [132,140]. Yasuni is the only protected area for the Near Threatened Golden-mantled Tamarin. Adequate data on bats and rodents in this region are not available to indicate whether it is a center of endemism for mammals overall.

Given the park’s extremely high plant richness, there is potential for a high number of regional plant endemics. Five species documented in Yasuni National Park have not been found anywhere else in the world: two herbaceous plants in the Begonia family, Begonia oellgaardii and Begonia sparronae; another herb, Tiquipina feoleta (Thimbiaceae), representing a new genus that lacks chlorophyll; and two trees, Tetrameranthus globiferus (Annonaceae) and Moreuni laxiflora (Meneyaceae) (Table 7 and [141]). In addition, dozens of plant collections from the park represent species new to science that experts have not yet named, and that may not have been collected elsewhere. Kreft et al. [93] found that at least 10% of the 313 vascular epiphytes in Yasuni are endemic to the upper Napo region. Balslev [142] provides another estimate for regional plant endemism. His study examined distribution patterns of plants that occur in Ecuador, and sampled plants representing various life histories and taxonomic families that had both accurate distribution and altitudinal data (n = 536). Included were 128 species known to occur in the Ecuadorian Amazon. Of these, 18% (23 spp.) were endemic to an area larger than, but overlapping with, the Napo Moist Forests ecoregion. Interestingly, Pitman et al. [101] documented an abrupt shift in tree community structure at the genus level near the Ecuador-Peru border, so tree communities in Yasuni are distinct from those in adjacent Peru. Together, these studies suggest that there are roughly ~400–720 regional endemic plant species in Yasuni (10%–18% endemism rate [93,142] ×4,000 estimated plant species in 10,000 km² in the plant richness center encompassing Yasuni [91]).

The total number of regionally endemic vertebrate species protected within Yasuni is not high compared to the numbers found in “biodiversity hotspots”—areas prioritized for conservation because of their endemism and vegetation loss [1]. However, the higher estimate for regionally endemic plant species protected in the park is just under 50% of the first threshold that qualifies an area as a biodiversity hotspot. The preliminary data are notable, given Yasuni’s small size relative to most of the biodiversity hotspots, and suggest that the Napo Moist Forests may be globally outstanding for plant endemism. Furthermore, Yasuni is the only stable national park that is currently protecting these regional endemics (see below).

### Yasuni’s Additional Conservation Values

Yasuni National Park is one of the most biodiverse places on Earth, whether assessed on a landscape or local scale, particularly for amphibians, reptiles, birds, bats, and trees. Part of this high

#### Table 8. Regionally endemic amphibians, birds, and mammals of Yasuni National Park.

| Class       | Species                        | Common Name                      |
|-------------|--------------------------------|----------------------------------|
| Amphibians  | Allobates insperatus           | –                                 |
|             | Allobates zaparo               | Zaparo Poison Frog               |
|             | Rhaebus sp. nov. 1             | –                                 |
|             | Ameerega bilinguis             | Ecuador Poison Frog              |
|             | Hyla varia                     | Santa Cecilia Rocket Frog        |
|             | Hyla varia sp. nov. 1          | –                                 |
|             | Hylosomantis hulli             | –                                 |
|             | Oscocephalus alboguttatus      | Whitebelly Treefrog              |
|             | Pristimantis auricolivatus     | –                                 |
|             | Pristimantis auricollinus      | –                                 |
|             | Pristimantis kichwarum         | –                                 |
|             | Pristimantis libratus          | –                                 |
|             | Pristimantis ophalthalmus      | Lago Agrio Robber Frog           |
|             | Pristimantis paululus          | Amazon Slope Robber Frog         |
|             | Pristimantis pseudocumatinus   | Sarayacu Robber Frog             |
|             | Pristimantis sp. 2             | –                                 |
|             | Pristimantis sp. 3             | –                                 |
|             | Pristimantis sp. 4             | –                                 |
|             | Pristimantis warmani           | –                                 |
| Birds       | Mitu salvini                   | Salvin’s Curassow                 |
|             | Anaides calopterus             | Red-winged Wood-Rail             |
|             | Geotrygon saphina              | Sapphire Quail-Dove              |
|             | Phaethornis atrimentsalis      | Black-throated Hermit             |
|             | Leucicus chlorocerus           | Olive-spotted Hummingbird        |
|             | Gallula tobinea                | White-chinned Jacamar             |
|             | Nonnula brunea                 | Brown Nunlet                      |
|             | Thanopholhus praecox           | Cocha Antshrike                   |
|             | Epinecrephyla fijolaasi         | Yasuni Antwren                    |
|             | Myrmotherula seminis           | Rio Suno Antwren                  |
|             | Herpsilochmus dugandi          | Dugand’s Antwren                  |
|             | Gymnadoplihus lunulata         | Lunulated Antbird                 |
|             | Gallaria dignissima            | Ochre-striped Antpitta            |
|             | Hylopenius fulvinirenus        | White-lored Antpitta              |
|             | Poecilothrix calopterus        | Golden-winged Tody-Flycatcher     |
|             | Tolmomyias traylori            | Orange-eyed Flycatcher            |
|             | Heterocercus aurantiavertex    | Orange-crested Manakin            |
|             | Cacicus scoleri                | Ecuadorian Cacique                |
|             | Oxyalus latirostris            | Band-tailed Oropendola            |
| Mammals     | Lophostoma yasuni              | Yasuni Round-eared Bat            |
|             | Sphiggurus ichillus            | Streaked Dwarf Porcupine          |
|             | Saginus triparius              | Golden-mantled Tamarin            |
|             | Pithecia equatorialis          | Equatorial Saki                   |

Regionally endemic amphibians and mammals are restricted to the Napo Moist Forests ecoregion [133]. Birds are restricted to Upper Amazon-Napo lowlands Endemic Bird Area or otherwise noted as regionally endemic by Ridgely and Greenfield [129]. Amphibian common names are from [224]. Only species known to occur in Yasuni National Park are included in the list.

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[1] Haffer, H. (1979). The birds of the Bolivian Amazon. Occ. Pap. Mus. Zool. Univ. Mich. 153, 1–221.

[2] Pitman, R. H., Fragoso, J. M. V., Sclater, J. P., & Fjeldsa, J. (1985). The Neotropical avifauna. Columbia University Press, New York.

[3] Ridgely, R. C., & Greenfield, P. (2002). The birds of Panama: the eastern theater, Vol. 1 - the songbirds. John Cramer, LLC, Ithaca, NY.

[4] Greenfield, P., & Greenfield, L. (2003). The birds of Ecuador: a field guide. Oxford University Press, New York.

[5] Smith, J. A., & Ramírez, J. (2004). The mammals of Ecuador: a guide and summary. Galápagos Conservation Trust, Quito, Ecuador.

[6] Greenfield, P., & Greenfield, L. (2005). The birds of Ecuador: a field guide. Oxford University Press, New York.

[7] Greenfield, P., & Greenfield, L. (2007). The birds of Ecuador: a field guide. Oxford University Press, New York.

[8] Greenfield, P., & Greenfield, L. (2008). The birds of Ecuador: a field guide. Oxford University Press, New York.

[9] Greenfield, P., & Greenfield, L. (2009). The birds of Ecuador: a field guide. Oxford University Press, New York.

[10] Greenfield, P., & Greenfield, L. (2010). The birds of Ecuador: a field guide. Oxford University Press, New York.

[11] Greenfield, P., & Greenfield, L. (2011). The birds of Ecuador: a field guide. Oxford University Press, New York.

[12] Greenfield, P., & Greenfield, L. (2012). The birds of Ecuador: a field guide. Oxford University Press, New York.

[13] Greenfield, P., & Greenfield, L. (2013). The birds of Ecuador: a field guide. Oxford University Press, New York.
Yasuní National Park

Threats to Yasuní’s Conservation Values

Despite its being a “strict” protected area, current and pending oil projects in Yasuní threaten all four of the key strengths outlined...
above. Ecuador is a small nation that relies on the oil industry for half of its total export earnings and for over one-third of its annual federal budget [159]. Three fields in Yasuní—Ishpingo-Tambo-cocha-Tiputini—contain ~850 million barrels of crude oil, or ~20% of Ecuador’s known reserves (the ITT Block; Figure 1B). In addition, adjacent Block 31 has significant reserves that could be developed with the potential for sharing ITT infrastructure. Thus, pressure to drill in ITT has understandably been intense.

In that context, the announcement of Ecuadorian President Rafael Correa in June 2007 to postpone ITT drilling plans and seek an alternative way forward was very progressive. Ecuador has calculated that government earnings from exploitation of ITT’s crude oil are roughly equivalent to the carbon market value of the oil, both around $7 billion [38]. Furthermore, the total value to Ecuador of pursuing the Yasuní-ITT Initiative is considerably higher, even from a strictly economic point of view. By precluding new oil production infrastructure and access routes, the Yasuní-ITT Initiative would help keep forests in this region intact, generating benefits through maintenance of forest carbon, ecosystem services, and biodiversity. Although no market valuation exists specifically for Yasuní, recognized economists, including Robert Costanza, have established that standing tropical forests offer significant financial value. The Yasuní-ITT Initiative will generate economic benefits even beyond the park. Ecuador plans to invest the carbon monies it receives from the Initiative not only in the management and conservation of Yasuní, but also in the country’s entire protected area network (SNAP) and indigenous territories, and in other conservation and sustainable development projects [38]. SNAP includes lands already prioritized as globally valuable investments for conservation dollars, including sizeable portions of the Tropical Andes and Tumbes-Chocó-Magdalena hotpots [1,160]. The Ecuadorian government now has a high-level team developing and promoting the Yasuní-ITT Initiative, making Ecuador’s revolutionary initiative a viable proposal on the international stage.

Explicit in the messaging of the Yasuní-ITT Initiative was the recognition of the potential threats oil production could pose to the biodiversity of the region. Threats come from both direct and indirect impacts [13,27,161,162]. Direct impacts of oil development include immediate deforestation for the project’s production plant, drilling platforms, access routes, and pipelines, along with contamination from any project-related spills, leaks, or accidents.

A preliminary study of potential environmental impacts from exploiting the ITT oil fields, conducted in 2007 by Ecuador’s state oil company, Petroecuador, revealed that direct impacts would likely be substantial. According to this report, the project would require a major processing facility (~6 ha), seven separate platforms (six for production and one for reinjection), and a new rail system to access these platforms, which would be spread along the entire length of the ITT block [163]. Oil-related
contamination threatens Yasuní’s large aquatic mammals, such as the Endangered Giant Otter and the Vulnerable Amazonian Manatee [116,122]. Both species have been documented in the Tiputini and Yasuní Rivers [117,164], which would likely be the principal access routes and infrastructure sites for oil development in ITT or the adjacent Block 31.

Compared to the direct impacts, the indirect impacts of new oil development in ITT or Block 31 are likely to be even greater: colonization and its subsequent secondary deforestation, fragmentation, and unsustainable hunting and fishing. All would intensify biodiversity loss. As indicated above, preliminary ITT development plans call for an extensive new transport and pipeline infrastructure. While plans reference train access, companies are much more likely to seek permits for building new roads, the most widespread and proven method of accessing land-based oil reserves. In either case, there would be unprecedented human access to one of the most intact portions of the Ecuadorian Amazon [13].

Indeed, oil development and its indirect impacts have played a major role in turning the Napo region into one of the 14 major deforestation fronts in the world [165]. Ecuador has had the highest deforestation rate of any Latin American country for several years [166,167]. Wunder [168] discussed how oil development typically decreases overall deforestation in a region, largely by reducing pressure from agricultural and logging interests. However, Ecuador was shown to be the primary exception to this phenomenon, mainly because the oil itself was located deep in primary forest and the extensive system of oil access roads opened the forest [168]. Access facilitated colonization and subsequent deforestation by small-scale migrant farmers pursing agriculture and cattle ranching [168–174], with an additional role played by indigenous peoples’ farming of commercial crops [174].

Prior to intensification of oil exploration in the 1970s, the total deforested area in the Ecuadorian Amazon was only ≈410,000 hectares (data [171], synthesized in [172]). Only 4.1% of the forests were within 5 kilometers of a road [174], the maximum distance for the practice of successful agriculture [175]. From 1986 to 2001, concentrated oil exploitation in northeastern Ecuador—with attendant in-migration, farming, and urbanization—resulted in deforestation averaging 40,000 hectares per year [172,174]. For each kilometer of road constructed, ≈120 hectares of agricultural lands have been cleared [174]. Unlike Brazil, agricultural lands in the Ecuadorian Amazon do not appear to be abandoned over time, but remain in use by colonists even as more areas are cleared [174]. By 2001, nearly 33% of the Ecuadorian Amazon was within 5 kilometers of a road [174]. Researchers have concluded that oil exploration, production, and associated road construction programs by the oil industry and the government are responsible for this fast-paced deforestation [168,176].

Within Yasuní, on-the-ground impacts from oil development have diverged from oil company intentions and their projections in Environmental Management Plans. Social conditions and pressures have affected the Plans in ways difficult to address. For example, the U.S.-based Maxus oil company sought innovations to control environmental impacts when developing Block 16 in Yasuní. From 1992 to 1993, the company constructed a 150-kilometer road—the Via Pompeya Sur-Iro or informally “Via Maxus”—from the Napo River’s southern shore, through Yasuní, and ending in the Waoarani Ethnic Reserve [30,177,178]. However, Maxus did not build a bridge connecting this road to Ecuador’s highway network [178], as Texaco had done when constructing the nearby Via Auca in the 1980s [179]. The Via Auca starts in Puerto Francisco de Orellana (El Coca) with a bridge crossing the Napo River and ends in Waoarani territory, and has been associated with extensive environmental and social change [26,179]. In contrast, to reach the Via Maxus, all trucks and equipment must cross the Napo River on barges [179]. The corporate intent was that this logistical obstacle to outsider vehicles and migrants would limit access, and thereby avoid colonization and secondary deforestation in the park [170].

In addition, the company’s Environmental Management Plan called for numerous controls on colonization, deforestation, and hunting [180]. For example, by placing the pipeline underground and by using an innovative “geogrid” plastic to stabilize the roadbed, deforestation would be reduced in two ways [177]. The right-of-way would be narrowed to 25 meters instead of the typical 60 meters, and the clearing to provide logs to stabilize the roadbed would be reduced by 70% compared to the extent typically lost for tropical road construction [180]. Remarkably, the Plan stated that the total area deforested for the Via Maxus, the secondary roads, and all installations would be only 400 hectares (4 km²) [180]. Checkpoints and ground patrols would control colonization, and high-resolution satellite imaging would be used regularly to verify control [180]. Corporate officials and contractors would be prohibited from purchasing meat, fish, or other products from the Waoarani [180]. Frequent audits would ensure compliance with this Plan [180].

Although most innovations were indeed implemented, environmental impacts in Block 16 in Yasuní from the Via Maxus have been significant [26,27,29–31,34]. The road has attracted indigenous migration and building of new villages near and within the park [27,29,30]. Deforestation has resulted, estimated at a rate of 0.11% per year, with that rate increasing over the years [29]. Proximity to the Via Maxus is the strongest spatial factor in predicting where deforestation is occurring [29]. A conservative model based on these data projects that 50% of the forest within two kilometers of the Via Maxus will be deforested by 2063 due to settlements and forest conversion [29]. That projected area would be at least 148 km² and 37 times greater than what Maxus had stated would be deforested in its Environmental Management Plan. Although forest loss is better controlled within the park than outside it [29,172], it is undermining Yasuní’s conservation values as a strict protected area and as a potential refuge for species migrating due to climate change.

Oil development and resulting impacts also threaten Yasuní’s wilderness characters and its largely intact mega-faunal assemblage. The Via Maxus fragmented the northeastern section of Yasuní from the rest of the park. Further fragmentation is occurring because the Via Auca is facilitating illegal logging in Yasuní [26,35]. Irreversible impacts on the park’s biodiversity may occur even faster from fragmentation than from deforestation, based on regional analyses [172,174]. Large predator species may need unfragmented forest areas as large as 1 million hectares to persist [181]. Rare species, such as the Near Threatened Jaguar, Margay, Short-haired Dog, and Golden-mantled Tamarin, are also susceptible to the effects of oil-industry-related deforestation and fragmentation [132,133,182,183].

The Via Maxus and transport provided by oil companies to indigenous hunters are facilitating increased hunting in Yasuní [30,31,33,34,145]. Although indigenous populations have hunted in this region for generations, there is evidence that hunting is now disrupting populations of large, keystone vertebrates. Local depopulation of the Endangered White-bellied Spider Monkey (Ateles belzebuth) has been documented along the road [30], and modeling of field takes by indigenous communities living along the road indicates that hunting of this primate is unsustainable, along with that of four other species: Red Howler Monkey (Alouatta seniculus), White-fronted Capuchin (Cebus albifrons), White-lipped Peccary (Tayassu pecari), and Poeppig’s Woolly Monkey (Lagothrix lagotricha)
A study from February 2005 to March 2006 registered 40% lower mammal abundance along the Via Maxus compared to a control area in intact forest distant from roads [31]. A new camera-trapping study is providing similar results [33]. At least 47 species of wildlife—mostly mammals and fish, but also birds and reptiles—have been sold by indigenous hunters at a new market at the entrance of this oil access road [34]. In sum, hunting is diminishing Yasuni’s conservation value in supporting an intact large-vertebrate assemblage. Also, given that many of the targeted large vertebrates are important seed dispersers, hunting could, over time, diminish Yasuni’s conservation value in maintaining animal and plant composition and diversity (A. Di Fiore and A. Link, unpub. data, [31,147,148]).

Clearly, impacts from oil development in this region cannot be fully controlled [27], irrespective of corporate intentions and innovations. These direct and indirect impacts have the potential to be region wide, as active and proposed oil blocks blanket not just much of eastern Ecuador, but virtually all of northern Peru as well (Figure 4C). A striking example from Ecuador illustrates the reality of this threat. A site known as Santa Cecilia, located just north of Yasuni, had some of the richest amphibian [41] and reptile [57] diversity in the world. This site is now completely deforested due to oil-related disturbance and colonization [172,184].

Implications for Conservation

Our findings on Yasuni’s biodiversity, its additional conservation values, and the documented impacts from oil development regionally and in the park itself form the scientific basis for the following five policy recommendations. 1) Permit no new roads nor other transportation access routes—such as new oil access roads, train rails, canals, and extensions of existing roads—within Yasuni National Park or its buffer zone. 2) Permit no new oil exploration or development projects in Yasuni, particularly in the remote and relatively intact Block 31 and ITT Block. 3) Create protected biological corridors from Yasuni to nearby higher-elevation Andean parks for species on the move due to climate change. 4) Create a system of strict protected areas and no-go zones (i.e., off-limits to oil exploration and exploitation) in the northern Peruvian Amazon. 5) Establish a protected corridor between Yasuni and Cuyabeno Wildlife Reserve that, together with the Peruvian reserves, would form a trans-boundary mega-reserve with Yasuni National Park at its core.

In regard to recommendations 4 and 5, we emphasize that Ecuador has already created two “untouchable zones” (“zonas intangibles” in Spanish) off-limits to oil activities, one in the southern part of Yasuni and the other just north of it in Cuyabeno. The former zone was created to protect Ecuador’s last indigenous peoples living in voluntary isolation, and anthropological evidence indicates that they cross the border into Peru as well [185]. Thus, areas off-limits to oil activities are needed in northern Peru not only to conserve its high biodiversity [101], but the territories of indigenous peoples as well.

In closing, we reiterate the conclusions of Malhi et al. [155] and Kilchen and Solórzano [20], that keeping the northern Amazon—home to the basin’s highest biodiversity and the region least vulnerable to climatic drying—largely intact as a biological refuge is a global conservation priority of the first order. If the world’s most diverse forests cannot be protected in Yasuni, it seems unlikely that they can be protected anywhere else.

Materials and Methods

We calculated the congruence of richness centers in South America for vascular plants, amphibians, mammals, and birds, the groups for which sufficient data were available. For amphibians, mammals, and birds, we used extent-of-occurrence maps. Bird data are from Ridgely et al. [186], mammal data from the Global Mammal Assessment [187], and amphibian data from the Global Amphibian Assessment [189]. Species presences for these three groups were summed across an equal area grid of 100 km² (10 km×10 km) to generate maps of species richness. While the species richness for vertebrates could be mapped on a continuous scale, the plant richness data, obtained from Barthlott et al. [91], are spatially aggregated into areas having a range of species richness (e.g., a spatial unit has between 2,000 and 2,000 spp./10,000 km²). We therefore restricted the analysis to match the form of the plant data. We defined a richness center for plants as any region containing ≥4,000 vascular plant species per 10,000 km². Only nine diversity centers worldwide reach this species density (three of which are in South America) [91]. These plant species richness centers cover 6.4% of South America, close to the 5% threshold used in similar studies (e.g., [189]). We used the same 6.4% area threshold to define richness centers for birds, mammals, and amphibians (i.e., the richest 6.4% of all grid cells for these groups were selected). The congruence of richness centers was determined by spatially overlaying the maps for the four taxa. The maximum value of four indicates congruent richness centers for all groups investigated.

We also conducted an extensive literature review of field studies investigating the biodiversity of Yasuni National Park (Yasuni), synthesized relevant information, and then compared it to published maps and field inventory research from around the globe. Results on species richness were grouped into two spatial categories: landscape-scale richness, typically of ≤10,000 km², and local-scale richness, of ≤100 km², but generally on the order of 100 hectares to a fraction of a hectare (after Whittaker [46] and Pitman et al. [23]). When comparing Yasuni’s landscape richness to that documented for other areas in field inventories and maps at this scale, we used species counts established for the entire park (~10,000 km²), as described below. Where total size of areas sampled was lacking in published field inventories for other regions, we calculated an estimated size by mapping the given study site locations on Google Earth 5.0 [49] and using the software to create a polygon inclusive of all sites.

We compiled lists of amphibian, reptile, bird, mammal, and plant species that occur in Yasuni National Park by collating published and unpublished inventory lists. Species richness data labeled in the text as “known,” “documented,” or “confirmed” refer to species actually collected, sighted, or otherwise known by experts to occur within the boundaries of Yasuni National Park, or collected from the Tiputini Biodiversity Station (TBS) directly adjacent to the park. Data labeled in the text as “expected,” “estimated,” or “projected” refers to species not documented within the park or TBS, but anticipated to occur there based upon expert analysis of range distributions or statistical analyses. Much information is from research at the Napo Wildlife Center and Yasuni Research Station, both located within Yasuni National Park, and from TBS (see Figure 1B).

The amphibian species list was based largely on inventories conducted at TBS and the Yasuni Research Station. The reptile list was based on inventories at TBS. D. F. Cisneros-Heredia conducted herpetofaunal inventories at TBS annually from 1997 to 2001, employing the following survey techniques: visual encounter transects, leaf-litter quadrats, pitfall traps, amphibian larval surveys, and random point sampling [52]. S. F. McCracken conducted amphibian inventories, using leaf-litter quadrat surveys, at TBS annually from 2002 to 2004, and canopy bromeliad patch sampling at TBS and the Yasuni Research Station in 2006 and
2006 (S. McCracken, unpub. data, [190]). Incidental amphibian and reptile observations recorded by D. F. Cisneros-Heredia and S. F. McCracken at TBS and by S. F. McCracken at the Yasuní Research Station were included in the amphibian and reptile species lists. Additional amphibian species records for Yasuní National Park were included from S. Ron [191]. In addition, confirmed records of reptiles and amphibians based on voucher specimens collected within Yasuní National Park and around TBS were included. For these, D. F. Cisneros-Heredia examined amphibian and reptile specimens deposited at the following herpetological collections: Museo Ecuatoriano de Ciencias Naturales (DHMECN), Universidad San Francisco de Quito (DFCH-USFPQ), Fundación Herpetológica “Gustavo Orell” (FHSO), National Museum of Natural History, Smithsonian Institution (USNM), and Universidad Católica del Ecuador (QCAZ). D. F. Cisneros-Heredia and S. F. McCracken updated the taxonomy of both lists. To generate a total of known, inferred, and projected amphibian species on a landscape scale for greater Iquitos, Peru (in 11,310 km²), data were extracted from IUCN Red List of Threatened Species [47].

The bird list combined tallies from the Napo Wildlife Center [70], TBS [J. C. Arvin et al., unpub. data, provided by K. Swing, [69]], and studies conducted in Block 31 [192]. Habitats for the Napo Wildlife Center list included a large river (the Napo River), river islands on the southern side of the Napo, the river’s edge, secondary and primary terra firme forest, and a clay lick. Habitats for the TBS list included terra firme forest, seasonally flooded forest, tree-fall gaps, the Tiputini River, and an oxbow lake. Documentation included tape recordings, photographs, sight records, auditory observations, and substantiated observations by recognized experts dating back to 1991. We counted only species for which documentation or reliable information was given. P. English reviewed and updated the taxonomy used.

The mammal list started with data from the Campos [193] list developed as part of the Ecuadorian government’s Yasuní management plan, and was augmented by data from Utteras and Jorgenson [194], Tirira [78], and Rex et al. [85]. The entire mammal list was then reviewed by A. L. Gardner, who provided additional species for the list and classified species as known, expected, probable, possible, doubtful, or incorrect for Yasuní National Park. Further additions to the list were provided by C. C. Voigt and T. H. Kunz (unpub. data), A. Di Fiore (unpub. data, [195]) and K. Jung (pers. comm.). Taxonomy was updated and standardized to follow Wilson and Reeder [196]. Species were then counted as known for Yasuní National Park if they were: documented by Rex et al. [85], specifically listed as occurring in the park by Tirira [78], classified as known for the park by A. L. Gardner, and/or observed with up-close certainty in the park or at TBS by K. Rex, T. H. Kunz, or C. C. Voigt. Species were counted as expected if they were documented by Rex et al. [85] and/or listed as occurring in Yasuní National Park by Tirira [78], but had tentative identifications (cf) or were new to science (sp. nov.). Species were also counted as “expected” if they were listed as such for Yasuní by A. L. Gardner (pers. comm.) and not yet documented there by other reliable sources. A final review of the list was done by A. Di Fiore, C. C. Voigt, and T. H. Kunz. We consider the final list as the only current, accurate source of total known and expected mammal species for Yasuní, both because of the extensive peer review process it underwent and its updated taxonomy.

A comprehensive plant list was not compiled de novo. Instead, we used totals from two comprehensive lists to be published shortly (G. Villa, unpub. data, H. Mogollon and J. Guevara, unpub. data) for known and expected vascular plant species in Yasuní. We did compile and verify our own known and expected threatened plant list. The preliminary list was compiled from a list of plant species of concern in Yasuní developed for Finding Species by H. Mogollon and J. Guevara (unpub. data) and from data in Valencia et al. [197]. This was then augmented and corrected by G. Villa, with known and expected presence in Yasuní verified in accordance with the definitions given above, using online plant lists and collection records from Aarhus University [196], Center for Tropical Forest Science [199], Chicago Field Museum [200], Finding Species [201], Missouri Botanical Garden [202], New York Botanical Garden [203], and the IUCN Red List of Threatened Species [47]. Where species names could not be verified in ITIS [204], they were verified in Jürgensen and León-Yáñez [205].

The number of expected fish species in Yasuní comes from a 1999 synthesis of publications and fish lists from Ecuador and neighboring countries by K. Swing (unpub. data). Conservation status for all species comes from the IUCN Red List of Threatened Species [47]. To determine endemic status, mammal range maps were reviewed from Tirira [78] and from the IUCN Red List of Threatened Species [47], and amphibian range maps from only the latter source. Boundaries of protected areas used in the figures are from the online 2007 World Database of Protected Areas, developed by UNEP-WCMC and the IUCN World Commission on Protected Areas.

Supporting Information

Text S1 Uncertainty of Species Richness Results

Found at: doi:10.1371/journal.pone.0008767.s001 (0.07 MB DOC)

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Author Contributions
Conceived and designed the experiments: MB MSF. Performed the experiments: MB MSF CNJ HK DFCH SFM NCP PE KS GV ADF CV TK. Analyzed the data: MB MSF CNJ HK DFCH SFM NCP PE KS GV ADF CV TK. Wrote the paper: MB MSF CNJ HK DFCH SFM NCP PE KS GV ADF CV TK. Designed and created figures: CNJ HK.

References
1. Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403: 853–858.
2. Mittermeier RA, Mittermeier CG, Brooks TM, Pilgrim JD, Knudtson M, et al. (2003) Wilderness and biodiversity conservation. Proceedings of the National Academy of Sciences of the United States of America 100: 13531–13536.
3. Gentry AH (1988) Tree species richness of upper Amazonian forests. Proceedings of the National Academy of Sciences of the United States of America 85: 136–139.
4. Terborgh JW, Robinson SK, Parker III TA, Munn CA, Pierpont N (1990) Structure and colonization of an Amazonian forest bird community. Ecological Monographs 60: 213–238.
5. Voss RS, Emmons LH (1996) Mammalian diversity in Neotropical lowland rainforests: A preliminary assessment. Bulletin of the American Museum of Natural History 230: 1–115.
6. Young BE, Stuart SN, Chanson JS, Cox NA, Boucher TM (2004) Disappearing jewels: The status of new world amphibians. Arlington: VA NatureServe. 53 p.
7. Erwin TL, Pimenta MC, Murillo E, Achero V (2005) Mapping patterns of biodiversity for butterflies across the western Amazon Basin: A preliminary case for improving conservation strategies. Proceedings of the California Academy of Sciences 56: 72-83.
8. Haagensen T, Perez CA (2005) Mammal assemblage structure in Amazonian flooded and unflushed forests. Journal of Tropical Ecology 21: 133–145.
9. ter Steege H, Pitman NCA, Phillips OL, Chave J, Sabatier D, et al. (2006) Continental-scale patterns of canopy tree composition and function across Amazonia. Nature 443: 444–447.
10. Soares-Filho BS, Nepstad DC, Curran LM, Correa GC, Garcia RA, et al. (2006) Modeling conservation in the Amazon Basin. Nature 440: 520–523.
11. Nepstad DC, Stickler CM, Soares-Filho BS, Merrif F (2008) Interactions among Amazon land use, forests and climate: Prospects for a near-term forest tipping point. Philosophical Transactions of the Royal Society B: Biological Sciences 363: 1737–1746.
12. Killeen TJ (2007) A perfect storm in the Amazon wilderness: Development and conservation in the context of the Initiative for the Integration of the Regional Infrastructure of South America (IIRSA). Arlington: VA Conservation International. 98 p.
13. Finer M, Jenkins CN, Pimm SL, Keane B, Ross C (2008) Oil and gas projects in the western Amazon: Threats to wilderness, biodiversity, and indigenous peoples. PLoS ONE 3(10): e3292. doi:10.1371/journal.pone.003292.
14. Perez CA, Terborgh JW (1995) Amazonian nature reserves: An analysis of the defensibility status of existing conservation units and design criteria for the future. Conservation Biology 9: 34–46.
15. Taco MF (2001) El Parque Nacional Yasuní. In: Jorge J, Rodrigues MC, eds. Conservación y desarrollo sostenible del Parque Nacional Yasuní y su área de influencia. Quito, Ecuador: Ministerio del Ambiente/UNESCO/Wildlife Conservation Society. pp 48–51.
16. Finer M, Vijay V, Ponce F, Jenkins CN, Kahn TR (2009) Ecuador’s Yasuní Biosphere Reserve: A brief modern history and conservation challenges. Environment: Research Letters 4: 034005 (15 p.). doi:10.1088/1748-9326/4/3/034005.
17. Albacec C, Espinosa P, Prado W (2004) Rapid evaluation of the Gran Yasuní Napo. Durham, NC: ParkWatch. 26 p.
18. United Nations Educational, Scientific and Cultural Organization (UNESCO) (2004) Monographs. UNESCO: Paris. France. Available: http://www.unesco.org/mabolls/hit/birds/directory/biores.asp?code = ECU+02&mode = all. Accessed 2009 July 15.
19. Pitman NCA (2000) A large-scale inventory of two Amazonian tree communities. Ph.D. Dissertation. Durham, NC: Duke University.
20. Killeen TJ, Soleróano LA (2008) Conservation strategies to mitigate impacts from climate change in Amazonia. Philosophical Transactions of the Royal Society B: Biological Sciences 363: 1081–1088.
21. Tsuiimoto H, Poulsen AD, Koskolauke K, Moran RC, Quintana C, et al. (2006) Linking forested patterns with soil heterogeneity and satellite imagery in Amazonian Ecuador. Ecological Applications 13: 352–371.
22. Valencia R, Foster RB, Villa G, Condit R, Svenning J, et al. (2004) Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. Journal of Ecology 92: 214–229.
23. Pitman NCA, Terborgh JS, Shinar MR, Núñez P, Nell D, et al. (2002) A comparison of tree species diversity in two upper Amazonian forests. Ecology 83: 3210–3224.
24. Olson DM, Dinerstein E (2002) The Global 200: Priority ecoregions for global conservation. Annals of the Missouri Botanical Garden 89: 199–224.
25. Olson DM, Dinerstein E, Canavari P, Davidson I, Castro GV, et al. (1998) Freshwater biodiversity of Latin America and the Caribbean: A conservation assessment. Washington, DC: Biodiversity Support Program. 61 p.
26. Jorgenson JP, Coppolillo P (2001) Trabajos de grupo: Grupo 1: Análisis de Amenazas. In: Jorgenson JP, Rodrigues MC, eds. Conservación y desarrollo sostenible del Parque Nacional Yasuní y su área de influencia. Quito, Ecuador: Ministerio del Ambiente/UNESCO/Wildlife Conservation Society. pp 194–211.
27. Scientists Concerned for Yasuní (2004) Technical advisory report: The biodiversity of Yasuní National Park, its conservation significance, the impacts of roads therein, and our position statement. 33 p. Available: http://www.findingspecies.org. Accessed 2009 July 25.
28. Franzen M (2006) Evaluating the sustainability of hunting: a comparison of tree species diversity in two upper Amazonian forests. Ecology 83: 3210–3224.
29. Franzen M (2005) Huaorani resource use in the Ecuadorian Amazon: Hunting, food sharing, and market participation. Ph.D. Dissertation. Davis, CA: University of California.
30. Greenberg JA, Kefauver SC, Stimson HC, Yeaton CJ, Ustin SL (2005) Satellite detection of bushmeat hunting in eastern Ecuador. Remote Sensing of Environment 96: 202–211.
31. Zapata-Ríos G, Sauri N, Urteaga B, Vargas J (2006) Evaluation of anthropogenic threats in Yasuní National Park and its implications for wildlife conservation. Journal of Wildlife Management 70: 47–57.
32. Maher JL, Espinosa S (2009) Camera trap photos reveal bushmeat hunting threat to jaguars in Ecuador. Mongabay.com. Available: http://news. mongabay.com/2009/0117-maher-ecws-jaguar.html. Accessed 2009 Feb 11.
33. Suarez E, Morales M, Cureva R, Urreras B V, Zapata-Ríos G, et al. (2009) Oil industry, wild meat trade and roads: Indirect effects of oil extraction activities on a protected area in north-eastern Ecuador. Animal Conservation 12: 364–373.
203. New York Botanical Garden (2009) C. V. Starr Virtual Herbarium. New York, NY: New York Botanical Garden. Available: http://sciences.nybg.org/science2/VirtualHerbarium.asp. Accessed 2009 July 25.
204. Integrated Taxonomy Information System (ITIS) (2009) Integrated Taxonomic Information System Online Database. Available: http://www.itis.gov. Accessed 2009 July.
205. Jørgenson PM, León-Yánez S (1999) Catalogue of the vascular plants of Ecuador. St. LouisMO: Missouri Botanical Garden. 1182 p.
206. Burnham RJ (2004) Alpha and beta diversity of lianas in Yasuní, Ecuador. Forest Ecology and Management 190: 43–55.
207. Vale MM, Cohn-Haft M, Bergen S, Pimm SL (2005) Effects of future infrastructure development on threat status and occurrence of Amazonian birds. Conservation Biology 22: 1006–1015.
208. Ridgely RS, Allnutt TF, Brooks T, McNicol DK, Mehlem DW, et al. (2003) Digital distribution maps of the birds of the Western Hemisphere, version 1.0. ArlingtonVA: NatureServe.
209. Val AL, Almeida-Val VMF (1995) Fishes of the Amazon and their environment: Physiological and biochemical aspects. Berlin, Germany: Springer-Verlag. 224 p.
210. Manokaran N, Seong QE, Ashton PS, LaFrankie JV, Noor NSM, et al. (2004) Pasoh Forest Dynamics Plot, Peninsular Malaysia. In: Losos EC, Leigh Jr. EG, eds. Tropical forest diversity and dynamism: Findings from a large-scale plot network. Chicago, IL: University of Chicago Press. pp 585–598.
211. Smithsonian Tropical Research Institute Center for Tropical Forest Science (CTFS) (No date) Plot Information Summaries. Panama City, Panama: CTFS, Available: http://www.ctfs.si.edu/site/. Accessed 2008 September 28.
212. Lum SKY, Lee SK, LaFrankie JV (2004) Bukit Timah Forest Dynamics Plot, Singapore. In: Losos EC, Leigh Jr. EG, eds. Tropical forest diversity and dynamism: Findings from a large-scale plot network. Chicago, IL: University of Chicago Press. pp 464–473.
213. Chuyong GB, Condit R, Kenfack D, Losos EG, Moser SN, et al. (2004) Korup Forest Dynamics Plot, Cameroon. In: Losos EC, Leigh Jr. EG, eds. Tropical forest diversity and dynamism: Findings from a large-scale plot network. Chicago, IL: University of Chicago Press. pp 506–516.
214. Co LL, Lagazaf DA, LaFrankie JV, Bartolome NA, Molina JE, et al. (2004) Palanan Forest Dynamics Plot, Philippines. In: Losos EC, Leigh Jr. EG, eds. Tropical forest diversity and dynamism: Findings from a large-scale plot network. Chicago, IL: University of Chicago Press. pp 574–584.
215. Leigh Jr EG, Loo de Lao S, Condit R, Hubbell SP, Foster RB, et al. (2004) Barro Colorado Island Forest Dynamics Plot, Panama. In: Losos EC, Leigh Jr. EG, eds. Tropical forest diversity and dynamism: Findings from a large-scale plot network. Chicago, IL: University of Chicago Press. pp 451–463.
216. Makana J, Hart TB, Längola I, Evange C, Hart JA, et al. (2004) Ituri Forest Dynamics Plots, Democratic Republic of Congo. In: Losos EC, Leigh Jr. EG, eds. Tropical forest diversity and dynamism: Findings from a large-scale plot network. Chicago, IL: University of Chicago Press. pp 492–505.
217. Vallejo MI, Samper C, Mendoza H, Otero JT (2004) La Planada Forest Dynamics Plot, Colombia. In: Losos EC, Leigh Jr. EG, eds. Tropical forest diversity and dynamism: Findings from a large-scale plot network. Chicago, IL: University of Chicago Press. pp 517–528.
218. Gunatileke CV, Gunatilleke IAUD, Ashton PS, Ezhugala AUK, Weerasekera NS, et al. (2004) Sinharaja Forest Dynamics Plot, Sri Lanka. In: Losos EC, Leigh Jr. EG, eds. Tropical forest diversity and dynamism: Findings from a large-scale plot network. Chicago, IL: University of Chicago Press. pp 599–608.
219. Kanzaki M, Hara M, Yamakura T, Ohtsuki T, Tamura MN, et al. (2004) Doi Inthanon Forest Dynamics Plot, Thailand. In: Losos EC, Leigh Jr. EG, eds. Tropical forest diversity and dynamism: Findings from a large-scale plot network. Chicago, IL: University of Chicago Press. pp 474–481.
220. Sun I, Hsieh C (2004) Nanjenshan Forest Dynamics Plot, Taiwan. In: Losos EC, Leigh Jr. EG, eds. Tropical forest diversity and dynamism: Findings from a large-scale plot network. Chicago, IL: University of Chicago Press. pp 564–573.
221. Bunyavejchewin S, Baker PJ, LaFrankie JV, Ashton PS (2004) Huai Kha Khaeng Forest Dynamics Plot, Thailand. In: Losos EC, Leigh Jr. EG, eds. Tropical forest diversity and dynamism: Findings from a large-scale plot network. Chicago, IL: University of Chicago Press. pp 482–491.
222. Thompson J, Brook N, Zimmerman JR, Waide RB, Everham III EM, et al. (2004) Luquillo Forest Dynamics Plot, Puerto Rico, United States. In: Losos EC, Leigh Jr. EG, eds. Tropical forest diversity and dynamism: Findings from a large-scale plot network. Chicago, IL: University of Chicago Press. pp 540–550.
223. Sukumar R, Suresh HS, Dattaraja HS, John R, Joshi NV (2004) Mudumalai Forest Dynamics Plot, India. In: Losos EC, Leigh Jr. EG, eds. Tropical forest diversity and dynamism: Findings from a large-scale plot network. Chicago, IL: University of Chicago Press. pp 551–563.
224. Frank N, Ramus E (1995) Complete guide to scientific and common names of reptiles and amphibians of the world. Pottsville, PA: N G Publishing Inc. 377 p.